https://doi.org/10.1590/1678-992X-2023-0294

ISSN 1678-992X

SCIENTIA AGRICOLA

100 Years on Boron Research in Plants – Soils and Plant Nutrition

Unfolding boron dynamics at the scale of soil-water-fertilizer-crop systems in the tropics: from soil availability to plant requirements

Cassio Hamilton Abreu-Junior[1]*, Juan Ricardo Rocha[1], Timóteo Herculino da Silva Barros[1], Gabriele Rossini Moreira[2], Vinícius Pires Rezende[2], Viviane Nunes dos Santos Cagliari[2], Carlos da Rocha Junior[2], Alyam Dias Coelho[2], Rodrigo Marcelli Boaretto[3], Gian Franco Capra[4], Thiago Assis Rodrigues Nogueira[5], Arun Dilipkumar Jani[6], José Lavres Júnior[2]

[1]Universidade de São Paulo/CENA – Divisão de Produtividade Agroindustrial e Alimentos, Av. Centenário, 303 – 13416-000 – Piracicaba, SP – Brasil.
[2]Universidade de São Paulo/CENA – Divisão de Desenvolvimento de Métodos e Técnicas Analíticas Nucleares, Av. Centenário, 303 – 13416-000 – Piracicaba, SP – Brasil.
[3]Instituto Agronômico de Campinas/Centro de Citricultura Sylvio Moreira, Rod. Anhanguera, km 158 – 13490-970 – Cordeirópolis, SP – Brasil.
[4]Università degli Studi di Sassari – Dipartimento di Architettura, Design e Urbanistica, Polo Bionaturalistico, Via Piandanna, 4 – 07100 – Sassari – Italy.
[5]Universidade Estadual Paulista/FCAV – Depto. de Ciência do Solo, Via de Acesso Prof. Paulo Donato Castellane s/n – 14884-900 – Jaboticabal, SP – Brasil.
[6]California State University/Monterey Bay – Dept. of Biology and Chemistry, Campus Center, 100 – 93955 – Seaside, CA – USA.
*Corresponding author <cahabreu@cena.usp.br>

Edited by: Tiago Tezotto

Received December 14, 2023
Accepted December 13, 2024

ABSTRACT: Boron (B) is an essential element that limits crop productivity and quality in tropical regions due to its low availability. Rainfall regime influences B dynamics in soil, which, in turn, affects crop responses to B. Tropical soils are considered low in B if concentrations are less than 0.20 and 0.60 mg kg^{-1} for annual and perennial crops, respectively. The B availability in soil is governed by the soil's pH, texture, organic matter (OM) content, cation exchange capacity, and source material. Plants' uptake of B occurs passively, although it varies according to its availability in the soil solution. The presence of low- affinity (BOR1 gene) and high-affinity (NIP5;1 gene) transporters has been characterized. B deficiency can impair crop development due to its role in cell metabolism at the molecular, physiological, anatomical, and morphological levels. Both B deficiency and toxicity affect plant growth, highlighting the importance of monitoring B availability by assessing soil fertility to optimize crop performance and quality. Further study should examine the nutritional management of economically important crops using B sources with different solubility in water, application rates, particle sizes, placement, forms, and timing. The speculation that the range between B deficiency and toxicity is narrow may be misunderstood, especially when foliar diagnosis is still neglected. This review aims to understand B dynamics in tropical soils, its functions in higher plants cultivated in these regions, and how its deficiency and/or toxicity can affect agricultural production.

Keywords: boron essentiality, boron management, food yield and quality, tropical soil

Boron bioavailability in tropical soil

Boron (B) is essential for complete vegetative and reproductive development (Marschner and Rengel, 2012). A comprehensive understanding of B dynamics at the soil-plant interface, along with the intricacies of its function in plants, is imperative for formulating effective management practices. These practices aim to ensure the efficient supply of B to crops, optimizing productivity. This is particularly crucial in tropical soils, where the natural availability of B is limited, resulting in impaired plant development (Mantovani et al., 2013).

Boron is distributed non-uniformly in the environment and occurs naturally through various sources, such as rocks, sediments, minerals, groundwater, and organic matter (OM). Mineral sources of B show low susceptibility to weathering, especially tourmaline, the most abundant and insoluble form of B (Das and Purkait, 2020; Malavolta, 1980). Notable natural B sources include colemanite (calcium borate), ulexite (calcium sodium borate), and borax (sodium borate) minerals (Das and Purkait, 2020). The chemical and biological reactions within the soil contribute to the solubilization of diverse mineralogical species, with those possessing higher sodium (Na) concentrations exhibiting heightened susceptibility to weathering (Botelho et al., 2022). Once solubilized in soil, B acts as a Lewis acid (Peak et al., 2003), reacting with water to form boric acid (H_3BO_3) (Soares et al., 2005) due to its tendency to accept electrons.

In tropical soils, B concentrations of 0.20 mg kg^{-1} in annual crops and 0.60 mg kg^{-1} in perennial crops are considered low (Cantarella et al., 2022). However, B is even lower due to factors such as pH, temperature, OM, texture, and the presence of other chemical elements in the soil, which is why the B concentration in the soil solution is in the order of µg kg^{-1} (Goldberg, 1997). In the liquid fraction of the soil, B can be present as boric acid (H_3BO_3) and borate anion ($B(OH)_4^-$). These two forms coexist in equilibrium, with the proportion of each dependent on soil pH (Shorrocks, 1997; Antoniadis et al., 2013). Consequently, the equilibrium between boric acid and borate anions, governed by soil pH, is a pivotal factor in determining B availability in the soil solution (Zhu et al., 2022):

$$B(OH)_3 + H_2O = B(OH)_4^- + H^+$$

Weathering is a primary factor in the formation of many tropical soils, which characteristically exhibit lower levels of silicates, higher levels of iron and aluminum (Al) oxides and hydroxides, and clay minerals with a 1:1 structure, such as kaolinite. The majority of inorganic colloidal particles resulting from pedogenesis possess high surface areas and numerous adsorption sites, with a predominance of positive charges. These soils are also characterized by lower pH values, where B is found predominantly as H_3BO_3, a weak acid (Soares et al., 2005). Substances lacking charge exhibit reduced interaction with the colloidal matrix of the soil, thereby decreasing the likelihood of absorption by plant roots. Consequently, in acidic soils, the absence of charge can promote increased leaching of nutrients (Cruz et al., 1987). This phenomenon underscores the importance of proper fertilization management, as the nutrient losses through leaching highlight the necessity for strategies to mitigate such losses and ensure optimal plant nutrient uptake.

Studies have shown that elevated pH levels favor the incorporation of the hydroxyl ions into H_3BO_3, thereby increasing the concentration of $B(OH)_4^-$ anions (Soares et al., 2005). This dynamic equilibrium between these two species, influenced by pH (Zhu et al., 2022), is crucial for understanding the sorption and desorption of B, which contributes to the maintenance of optimal B availability in soil solutions (Strawn, 2021). The optimal pH range for maximizing B availability in the soil solution is reported to be between 7 and 9 (Soares et al., 2008). Beyond these values, a competitive dynamic emerges between hydroxyl ions and $B(OH)_4^-$ anions for the positive sites on colloidal particles (Cruz et al., 1987), reducing the adsorption of the targeted species.

In tropical soils, attaining pH values greater than 6 under natural conditions is challenging. Consequently, liming is required to raise the pH level in the soil. Intriguingly, this process can enhance the levels of calcium (Ca^{2+}) and magnesium (Mg^{2+}) in soil, which can interact with the bivalent anion $B(OH)_4^-$, leading to the precipitation of B. Other processes that reduce B bioavailability include B fixation, which can occur under both natural conditions and following liming application. Additionally, the formation of inner-sphere complexes, where B is incorporated into the crystalline network of mineral particles under certain conditions, is a process that is difficult to reverse (Strawn, 2021).

The decomposition of OM has been demonstrated to enhance B soil levels. This augmentation can be achieved through two primary mechanisms: the direct release of B or the formation of organic surfaces capable of interacting with $B(OH)_4^-$ ions. Notwithstanding the predominant negative charge of OM, it exhibits the capacity to adsorb $B(OH)_4^-$ through diverse mechanisms, encompassing surface interactions or charge variations. Furthermore, OM has been observed to produce humic compounds and fulvic acids, which have been shown to form stable complexes with B, thereby limiting its availability for plant uptake (Chaudhary et al., 2005). However, in spite of these interactions, OM is associated with an increase in B bioavailability, as it has been demonstrated to adsorb higher levels of B compared to the mineral constituents of soil (Goldberg, 1997).

A global investigation has been conducted into the correlation between soil types and B availability (Shorrocks, 1997). The following soil conditions have been associated with B deficiency: 1) highly weathered soils (e.g., Podzols, Acrisols, and Ferralsols); 2) soils with fine particles situated on calcareous materials (e.g., Calcisols); 3) soils with a predominantly sandy texture (e.g., Arenosols); few developed soils (e.g., Leptosols); and 4) soils developed from volcanic ash (e.g., Andosols). Tropical regions encompass 38 % of the global land surface and include significant areas across Africa (43 %), South America (28 %), Asia (20 %), Australia (5 %), and Central and North America (4 %). In these regions, B deficiency frequently occurs due to the composition of the parent material and the texture of the soil. Notable instances of B deficiency in soil include several countries, namely China, India, Sri Lanka, Cameroon, Nigeria, Belarus, Estonia, Lithuania, Russia, Finland, Sweden, Denmark, Germany, Poland, Brazil, Chile, United States, and Canada (Shorrocks, 1997).

For instance, in the tropical country of Brazil, 70 % of the soils are classified as Ferralsols, Acrisols, and Arenosols (Santos et al., 2011). A natural scarcity of available B characterizes these soils and are predominantly distributed across several states in Brazil, including Bahia, Ceará, Goiás, Minas Gerais, Pernambuco, Mato Grosso, Mato Grosso do Sul, Paraná, Rio Grande do Sul, Santa Catarina, and São Paulo (Epstein, 1972). The region's predominant crops include cotton (*Gossypium herbaceum* L.), coffee (*Coffea* sp.), sugarcane (*Saccharum officinarum* L.), citrus (*Citrus sinensis* (L.) Osbeck), pine (*Pinus elliottii* Engelm.), and soybean (*Glycine max* (L.) Merrill).

Boron extraction and determination in soil

There is considerable speculation regarding the underlying factors that result in the narrow range between B deficiency and toxicity. The limits between these extremes are subject to variation based on environmental and intrinsic factors specific for each crop. In tropical soils with a characteristic acidic pH, B is predominantly present as H_3BO_3, a form that exhibits high solubility. In contrast, in alkaline soils with elevated pH levels, B exhibits increased adsorption potential, reducing plant availability.

Various methodologies exist for extracting and determining B in soil, each exhibiting distinct advantages. For instance, the hot water and diethylene glycol extraction methods (van Raij et al., 2001) have been particularly effective. In the context of tropical acid soils, a method that employs plastic bags and a microwave oven for heating, in conjunction with a 1.25

g L^{-1} barium chloride extractant solution, has been proposed (Abreu et al., 1994; Chaves et al., 2006). This method, officially employed in Brazil, a tropical country, and also known as the "hot water method", utilizes colorimetry, molecular absorption spectrophotometry, and plasma atomic absorption spectrometry to determine B (ICP-AES) (Abreu et al., 2001).

The available B extracted by hot water has been shown to exhibit a higher degree of correlation with the B content plants and crop yield (Abreu et al., 2001; Moreira et al., 2010), suggesting that a classification system based on this method would be a reliable means of discussing B deficiency or toxicity in tropical soils. For annual crops, the following classes of interpretation for B availability in soil, determined by hot water method, in mg kg^{-1} have been established: 0.0-0.2 as low, 0.21-0.6 as medium, 0.61-1.1 as high, 1.2-3.0 as very high, and > 3.0 as toxic (Abreu et al., 2005). However, such classification does not exist for B availability in soil, determined by the hot water method, for perennial crops, indicating the necessity for further research in this field.

Uptake and transport of boron by plants

The most effective method of absorbing B is through the roots, with passive mechanisms predominating. However, this route can vary depending on the B concentration in the solution, potentially resulting in expenditures to enhance B absorption. In the soil-plant system, plants predominantly absorb H_3BO_3, with the highest concentrations observed at the tips of older leaves due to the plant's transpiration flow (Luo et al., 2024). Following absorption by the roots, B becomes mobile in the xylem. Upon reaching the plant's apex, it becomes immobilized, primarily within the cell walls, exhibiting minimal redistribution (Coskun and White, 2023).

In the context of Eucalyptus (*Eucalyptus grandis* W. Hill*)* clone seedlings, mass flow has been identified as the predominant mechanism of B transport in the soil. Diffusion, however, plays a complementary role, exhibiting greater relative importance in soils with limited B availability and during periods of water deficit (Mattiello et al., 2009).

Nutritional disorders resulting from B deficiency are prevalent in tropical soils (Rosolem et al., 2001), underscoring the significance of effective B management. Given the necessity of B fertilization, as OM is the predominant source of B in soil (Schmidt et al., 2021), addressing B deficiency is crucial for enhancing crop productivity. In tropical sandy soils, the low concentrations of OM and clay reduce the retention of B and lead to higher leaching, which further diminishes B availability. This reduced availability of B can significantly affect crop productivity (Yermiyahu et al., 2001). Additionally, the movement of B from the roots to the leaves is highly dependent on transpiration, a process influenced by environmental factors such as temperature, humidity, and soil moisture. These environmental factors regulate the long-distance transport of B in the xylem, emphasizing the impact of tropical climates on B uptake and its subsequent influence on plant growth (Takano et al., 2008; Reid, 2014).

Once deposited in the leaves, the remobilization and redistribution of B via the phloem is restricted and complex, settling in the apoplast. However, in plant species that produce sugar alcohols containing cis-hydroxyls capable of binding to the B-Pyl complex, B can move along the polyol flow and be translocated via the phloem to the new leaves (Tanaka and Fujiwara, 2008). The mobility of B in the phloem of certain plants, including apples, plums, cherries, and broccoli, has been documented. Consequently, the concentration of B in leaves of varying ages indicates its mobility (Brown and Shelp, 1997).

Plants experiencing B limitation have been observed to employ a variety of mechanisms for transporting H_3BO_3, including passive diffusion through the lipid bilayer, which has been found to have a high permeability coefficient with H_3BO_3, active transport by the BOR transporter, t he first transporter via the xylem participating in the distribution of B in the shoots, and transport facilitated by the NIP channel, which is responsible for H_3BO_3 absorption (Tanaka and Fujiwara, 2008; Miwa and Fujiwara, 2010) (Figure 1).

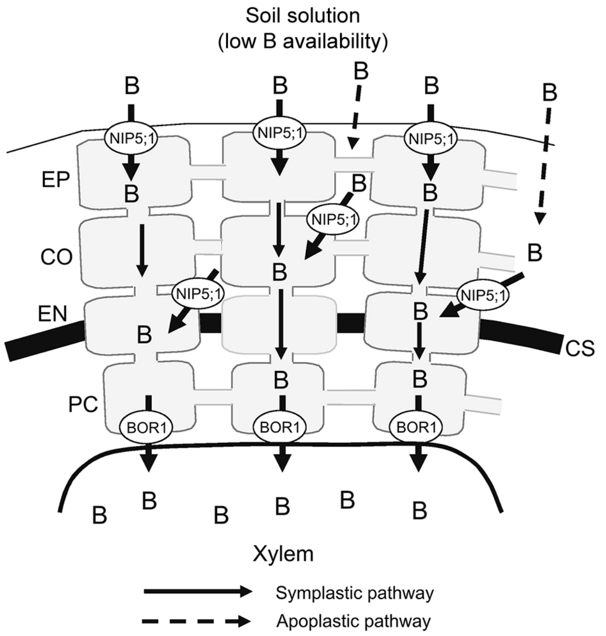


Figure 1 – Radial (or short distance) transport of boron (B) from soil solution, with epidermis at the top, through plant root, with xylem vessels at the bottom. The NIP5;1 gene is expressed in epidermis, cortex, and endodermis, or act as an uptake channel to B enter into the cytosol. Xylem B loading efflux transporter is made by the BOR1 gene, in the stele. EP = epidermis; CO = cortex; EN = endodermis; CS = casparian strip; PC = pericycle (Figure taken from Tanaka and Fujiwara, 2008 - https://doi.org/10.1007/s00424-007-0370-8).

Functions of boron in plants

Inadequate B availability has been demonstrated to exert a detrimental effect on crop yield (Brdar-Jokanovic, 2020). Consequently, B limits agricultural productivity worldwide (Gupta, 1993). The optimal amount of B in tissues varies between 30 and 75 mg kg^{-1}, but the amounts differ considerably between plant species (Arunkumar et al., 2018). The accumulation of B is associated with the amount of pectin in the cell wall, and these values for B content are generally higher in dicotyledons than in monocotyledons (Blevins, 2009).

Boron plays a multifaceted role in plants' physiological, structural, and hormonal processes. In the case of cotton, for instance, B has been observed to be involved in several critical processes, including carbohydrate metabolism, sugar transport, water relations, nitrogen (N) and auxin metabolism, tissue development and differentiation, cell wall formation, and plant reproduction (Cordeiro et al., 2022). It has been demonstrated that B enhances the synthesis of cell walls, contributing to the structural integrity and functionality of plasma membranes through the formation of a borate diol diester bond with apiose residues of rhamnogalacturonan II (RG-II). This process directly influences cell wall development, thereby affecting overall plant development (Bolaños et al., 2023; Hu and Brown, 1997). Furthermore, the incorporation of B into plant nutrition has been shown to enhance their resistance to diseases.

The application of B to maize (*Zea mays* L.) plants has been demonstrated to enhance pollen tube length after germination (García-Hernández and López, 2005). In addition, research conducted on rice (*Oryza sativa* L.) has indicated that B enhances pollen viability (Garg et al., 1979). Conversely, B deficiency has been observed to cause damage to the plasma membranes of plants, given its role in regulating membrane functions and its high concentration in the cell wall (Marschner and Rengel, 2012). Research has demonstrated that B deficiency impedes the assembly of hydroxyproline-rich glycoproteins in the cell wall of pollen tubes and contributes to the underdeveloped state of anthers and pollen (García-Hernández and López, 2005).

Boron deficiency in citrus plants has been shown to result in decreased plant growth and increased leaf-specific weight. This phenomenon can be attributed to the functional characteristics of this micronutrient (Han et al., 2008). In legumes, such as soybeans and beans, in addition to the aforementioned functions, the deficiency may affect the cell wall of the nodules present in the roots, hindering the work of diazotrophic bacteria. This is because the deficiency allows oxygen to enter the nodules, leading to low efficiency of biological N fixation (Lukaszewski and Blevins, 1996).

Molecular responses of boron deficiency and toxicity in plants

At the molecular level, B has been shown to play a role in various processes, including cell wall synthesis, the regulation of gene expression, transport of sugars, regulation of the cell cycle, and calcium metabolism (Brdar-Jokanovic, 2020). Cultivars exhibit different capacities for growth in soils with high B concentrations, which is uncommon in tropical regions but can occasionally be observed in poorly managed areas, where excessive applications of fertilizers containing B are made to compensate for the deficiency in soil. Wheat (*Triticum vulgare* Vill.) and barley (*Hordeum vulgare* L.) varieties that demonstrate tolerance to excess of B have been identified, exhibiting reduced B concentrations in their tissues compared to those classified as sensitive. The underlying mechanisms that confer B tolerance in these cultivars, leading to reduced B accumulation, can be attributed to enhanced B efflux capacity. This enhanced efflux is facilitated by the presence of transporters that remove B from cells (BOR genes) and/or the suppression of B entry channels (NIP5 and PIP1 genes) (Martínez-Cuenca et al., 2015).

Research on barley and wheat has demonstrated that tolerant varieties exhibit elevated expression of genes such as BOR2, which play a pivotal role in sequestering excess B within the vacuole. This sequestration within the vacuole renders the B less toxic to cellular processes (Miwa et al., 2008; Takano et al., 2008). The vacuolar sequestration mechanism enables the plant to accumulate higher concentrations of B without significant disruption to physiological functions. In addition to vacuolar compartmentalization, other mechanisms of B tolerance have been documented. One key mechanism involves morphological changes in the roots, including an increase in the concentration of reducing sugars, which helps sustain root growth even under B toxicity conditions. This process ensures continued water and nutrient uptake, aiding plant survival in B-rich environments (Aquea et al., 2012; Reid and Fitzpatrick, 2009). Another significant mechanism involves the role of transcription factors in regulating the expression of genes responsive to B stress, thereby enhancing the plant's capacity to tolerate elevated B concentrations (Miwa and Fujiwara, 2010; Reid, 2014).

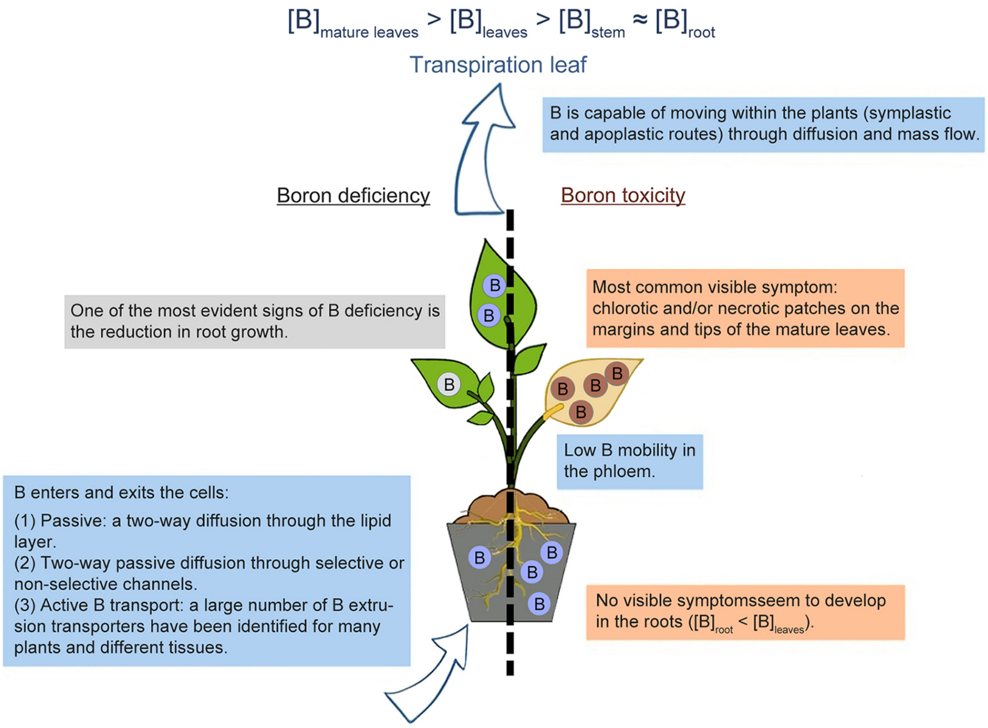
However, the levels of B tolerance exhibited by different cultivars cannot be fully explained by the accumulation of B in the leaves alone. Studies suggest that the role of B in plant metabolism is more intricate, involving the stabilization of molecules with cis-diol groups, such as RG-II and specific glycoproteins (Brown et al., 2002; O'Neill et al., 2004). The involvement of B in the structural integrity and function of the cell wall and plasma membrane is critical for maintaining various physiological processes. For instance, B contributes to the cross-linking of pectin in the cell wall, which strengthens the wall's rigidity and regulates ion exchange and nutrient transport (Koshiba et al., 2013). Furthermore, B plays a significant role in facilitating transport reactions, including the movement of ions, metabolites, and hormones across cell membranes (Brdar-Jokanovic, 2020; Goldbach et al., 2001). These multifaceted roles of B in stabilizing cellular structures and supporting membrane functions highlight its critical influence on plant growth and stress tolerance, underscoring the complexity of B metabolism beyond mere accumulation.

Boron deficiency has been shown to trigger molecular responses essential for plant survival in environments with low B availability. Among the primary responses is the downregulation of genes responsible for B transport, such as BOR1 and NIP5;1, which hinders B uptake and translocation from the roots to the shoots (Miwa and Fujiwara, 2010; Takano and Tanaka, 2023). This restriction in B transport further exacerbates the deficiency, leading to a disruption in cellular homeostasis. In response, plants activate antioxidant defense pathways, with upregulation of genes coding for enzymes like superoxide dismutase (SOD) and peroxidase (POD) to mitigate the oxidative stress caused by reactive oxygen species (ROS) accumulation under B-deficient conditions (Bolaños et al., 2023). These ROS scavenging mechanisms are vital for reducing cellular damage; however, they are not always sufficient to prevent long-term damage in severe B-deficient soils.

Boron has been demonstrated significantly impact cell wall formation, as it impairs the cross-linking of RG-II pectin. This process that is crucial for maintaining cell wall integrity. This weakens cell walls and affects various molecular pathways in growth and development, particularly in tropical crops such as maize and coffee (O'Neill et al., 2004). Furthermore, the genes involved in reproductive development exhibit heightened sensitivity to B deficiency, often resulting in abnormal floral organogenesis and reduced fertility due to impaired pollen tube growth and fertilization processes (Aasim et al., 2022). These molecular responses are pivotal in elucidating the limitations of B availability in tropical soils and the development of crop varieties capable of better tolerating B-deficient conditions.

Physiological responses of boron deficiency and toxicity in plants

Physiologically, B has been demonstrated to influence a variety of processes, including the absorption of other nutrients, enzyme activity, respiration, photosynthesis, transpiration, seed germination, fruit set, and resistance to biotic and abiotic stresses (Figure 2) (García-Sánchez et al., 2020; Ferreira et al., 2021; Prado, 2021; Mehran et al., 2023). The impact of B on plant biology is further demonstrated by its capacity to modify the structure of the plasma membrane, thereby modulating the activity of the H-ATPase of the plasma membrane and, consequently, stimulating the absorption of nutrients by the root system of the plant (Ferreira et al., 2021; Souza et al., 2022).



B is capable of moving within the plants (symplastic and apoplastic routes) through diffusion and mass flow.

Most common visible symptom: chlorotic and/or necrotic patches on the margins and tips of the mature leaves.

One of the most evident signs of B deficiency is the reduction in root growth.

Low B mobility in the phloem.

B enters and exits the cells:
(1) Passive: a two-way diffusion through the lipid layer.
(2) Two-way passive diffusion through selective or non-selective channels.
(3) Active B transport: a large number of B extrusion transporters have been identified for many plants and different tissues.

No visible symptomsseem to develop in the roots ($[B]_{root} < [B]_{leaves}$).

Figure 2 – Symptoms of boron (B) toxicity and deficiency in plants (Figure adapted from García-Sánchez et al., 2020 - https://doi.org/10.1016/j.jhazmat.2020.122713).

Several studies have investigated the impacts of B on plant growth and development, along with the mechanisms involved in the absorption, transport, and metabolism of this micronutrient (Hu and Brown, 1997; Takano et al., 2008; Reid, 2014; Aftab et al., 2022). Stress caused by B deficiency, a prevalent abiotic stress factor in tropical and subtropical soils, has been shown to impact the growth and development of citrus plant, including the trifoliate orange tree (*Poncirus trifoliata* L. Raf.), a significant citrus rootstock. In this species, long non-coding RNAs have been identified as regulators of metabolism and signal transduction of plant hormones, contributing to a tolerance mechanism against this stress (Zhou et al., 2019).

Boron deficiency has been observed to alter the vascular tissues of coffee trees, potentially resulting in the reduction of thickness in the xylem walls. This phenomenon has been shown to manifest in a decline in the number of stomata on the leaves, exhibiting malformations. Furthermore, the coffee tree's root system may undergo reduction, which has been observed to lead to an increase in flower abortion, thereby compromising fruit formation, and reducing crop productivity (Rosolem and Leite, 2007; Souza et al., 2022).

The most evident indication of B deficiency is a reduction in root growth (García-Sánchez et al., 2020). B deficiency has been shown to induce changes in root morphology, which can impact the synthesis of indoleacetic acid within the root, the translocation of sugars, the metabolism of carbohydrates, and the synthesis of nucleic acids. These changes can lead to an increase in the leaf/root ratio or a thickening of the root cell wall. This phenomenon is attributed to the accumulation of cellulose, amino acids, phenols, and lignin (Mesquita et al., 2016). The interruption of root growth observed in conditions of B deficiency results from inhibition of DNA synthesis, due to pyrimidine base deficits (Blevins and Lukaszewski, 1998). This can lead to a complete inhibition of nutrient absorption and transportation. In addition, a decline in antioxidant enzymes, such as SOD, POD, catalase (CAT), and ascorbate peroxidase, along with a decrease in the photosynthetic rate, transpiration rate, stomatal conductance, leaf gas exchange, and intercellular CO_2, has been documented (Wimmer and Eichert, 2013).

However, excessive B accumulation has been shown to induce a range of physiological disturbances in plants. Initial symptoms include chlorosis and necrosis at the leaf tips and margins due to cellular damage (Aquea et al., 2012). High B concentrations have been demonstrated to disrupt membrane integrity, leading to increased ion leakage and altered permeability, which hampers nutrient uptake and transport (Reid, 2014). This disruption in cellular homeostasis has been shown to induce oxidative stress due to the overproduction of ROS, which in turn causes damage to lipids, proteins, and DNA (Ardic et al., 2009).

In response to B toxicity, plants often upregulate antioxidant defenses, such as SOD and CAT activities. However, these defenses are sometimes insufficient to fully counteract the damage. B toxicity also impairs photosynthesis by affecting chlorophyll content and stomatal conductance, which reduces overall growth and productivity (Choudhary et al., 2020). In severe cases, B toxicity interferes with root development, diminishing root biomass and function and further compromising water and nutrient absorption (Riaz et al., 2022). This broad impact underscores the importance of balancing B levels to maintain plant health and productivity, given its role in various physiological processes and its potential for inducing stress under both deficiency and excess conditions.

Morphological responses of boron deficiency and toxicity in plants

Morphologically, B affects the architecture of the plant, the formation of roots, leaves, and flowers, as well as the fruit's size, shape, and quality. An excess or deficiency of B can negatively affect plant growth and productivity. B deficiency can also produce damage that negatively influences crop production and quality. In citrus orchards, B deficiency is a prevalent issue on a global scale, often coinciding with limited soil B availability and environmental stressors, such as drought or excessive rainfall (Ferreira et al., 2021).

Boron deficiency in soil has been demonstrated to inhibit root growth in pumpkin (*Cucurbita pepo* L.) seedlings. However, the supply of B has been shown to facilitate the resumption of expected growth in these seedlings. In addition, B-deficient seedlings have been observed to exhibit changes in their reproductive organs, which can affect fruiting and flowering. These alterations include wrinkled anthers, ruptured pollen tubes, and damaged flower buds (Zhou et al., 2014).

Boron deficiency has been identified as the most limiting nutritional disorder related to micronutrients in cotton (*Gossypium hirsutum* L.). This condition has been shown to result in substantial productivity losses, underscoring the potential for nutritional disorders related to B deficiency to adversely impact cotton yield and fiber quality (Souza Junior et al., 2023). Consequently, plants exhibit a greater demand for B during the reproductive phase than the vegetative phase (Prado, 2021).

In plants exposed to B excess, the most prevalent symptom is the presence of burns, which manifest as chlorotic and/or necrotic spots, often observed on the margins and tips of mature leaves. In contrast to the leaves, no visible symptoms develop in the roots, given the relatively lower concentration of B, even in soils with high B levels. The characteristic symptoms are not evident in species where B is re-translocated through the phloem. In such cases, dead apical shoots, abscission of young shoots, and lesions manifesting as dry, brown spots on the side of stems and petioles has been observed. Grafting has emerged as a prevalent technique to circumvent B toxicity (Sarafi et al., 2017; Simón-Grao et al., 2018).

Boron interaction with other nutrients

The interaction between B and N has implications for B availability. Elevated concentrations of N in the soil and plant leaves have been observed to result in B deficiency in the plant leaves (Long and Peng, 2023). The influence of B on the absorption and distribution of N varies according to the N source. Ammonium salt and nitrate are vital sources of inorganic N. Plants excrete protons while absorbing ammonium salt, leading to a reduced pH in the rhizosphere, and B exists mainly in the form of $B(OH)_3$ in the rhizosphere soil. The pH of the rhizosphere increases when plants absorb nitrate, and the B in the rhizosphere soil is converted primarily into $B(OH)_4^-$ (Gerendas et al., 1997). Consequently, plants absorb less B when nitrate is the N source than when ammonium salt is the N source (Long and Peng, 2023).

Research on tomatoes and maize indicates an antagonistic relationship between B absorption and phosphorous (P) absorption. This competitive relationship may be attributed to the same absorption and transport system of phosphate and borate (Kaya et al., 2009; Günes and Alpaslan, 2000). Furthermore, B deficiency has been observed to exacerbate the adverse effects of P deficiency and excess on physiological processes, including a decline in biomass and ribonuclease activity (Chatterjee et al.,1990).

Some studies have demonstrated that the potassium (K) concentration in citrus trees has been observed to increase in response to the application of B to the soil (Mattos Junior et al., 2024). This phenomenon is likely attributable to the role of K in maintaining the charge balance within root cells (Shabala et al., 2016). A correlation has been observed between the retention of K by citrus plants nourished with B and the increase in the activity of the ATPase enzyme that modulates the H^+ of the plasma membrane. This finding underscores the significance of B for plant nutrition (Ferreira et al., 2021).

The Ca-B ratio is a standard metric for evaluating the abundance of B in plants, and the optimal Ca-B ratio for the growth of different plants varies due to intraspecific and interspecific differences in nutritional requirements. The Ca-B interaction may closely correlate with cell wall-related physiological processes, given the vital roles of Ca and B jointly stabilizing and maintaining cell wall structure and function. Furthermore, B deficiency has been demonstrated to alter the intracellular concentration of Ca^{2+} and affect the expression of genes related to Ca^{2+} signal transduction. This suggests that the influence of B on Ca^{2+} signal transduction may be an important manifestation of the Ca-B interaction (González-Fontes et al., 2014).

The application of B fertilizers to a variety of plants has been shown to greatly mitigate the symptoms of Al toxicity, including inhibited root growth, blocked photosynthesis, and impaired activity of relevant enzymes (Riaz et al., 2022). This process has been observed to reduce Al accumulation in the cell wall and Al uptake, thereby alleviating Al toxicity. Different mechanisms of alleviation of Al toxicity by B have been observed in other plants. For instance, the application of B fertilizers to *Z. mays*, *Cucumis sativus* L., and *P. trifoliata* have been shown to mitigate Al-induced oxidative stress (Taylor and Macfie, 1994; Riaz et al., 2022).

Boron in the soil, recommendations, and boron fertilization

Soil analysis for micronutrients serves as a tool to guide fertilization and should be used with specific information about the species or varieties cultivated (Cantarella et al., 2022). In tropical regions, such as Brazil, where soils are highly weathered and have low levels of OM, the lack of B can be visible in plants (Prado, 2021). The interpretation of B availability classes, employing hot water as an extractant, in the soil for annual crops differs from those for perennial crops, as do the recommendations for Cerrado soils (Table 1) (Sousa and Lobato, 2004; Cantarella et al., 2022).

The recommendations for fertilization with B for crops cultivated in tropical soils exhibit variability according to the cultivar. Some studies have indicated that the recommendations for B fertilization are frequently expressed within a relatively narrow range between deficiency and toxicity. However, it is noteworthy that the ranges for certain other micronutrients (Table 2), such as copper (Cu) and manganese (Mn), are even more limited in scope, with their ranges between deficiency and toxicity being particularly constricted. For instance, research has demonstrated that Cu deficiency or excess can

Table 1 – Interpretations of boron (B) availability according to the regional bulletins of Brazil.

Concentration	Cerrado (Brazilian Savanna)[1]	Annual species[2]	Perennial species[2]
	-------------------------- B (mg kg^{-1}) --------------------------		
Low	0-0.30	0-0.20	< 0.60
Medium	0.30-0.50	0.21-0.60	0.60-1.00
High	> 0.50	> 0.60	> 1.00

[1]Sousa and Lobato (2004). [2]Cantarella et al. (2022).

Table 2 – Boron (B), copper (Cu), and zinc (Zn) acceptable ranges in leaves of different crops in tropical soils.

Crop		B	Cu	Zn
		-------------- mg kg^{-1} --------------		
Gossypium hirsutum	Cotton	40-60	5-25	25-100
Oryza sativa	Rice	4-25	3-25	10-50
Musa spp.	Banana	10-25	7-20	15-30
Coffea arabica	Coffee	60-100	10-20	20-40
Saccharum spp.	Sugarcane	5-15	5-15	10-30
Eucalyptus grandis	Eucalyptus	25-50	3.5-5.5	15-25
Zea mays	Maize	7-17	6-15	20-50
Glycine max	Soybean	21-55	10-30	20-50

Source: Cantarella et al. (2022).

Table 3 – Boron (B) fertilizer recommendations for the main Brazilian crops in the states of Bahia, Ceará, Goiás, Minas Gerais, Mato Grosso, Paraná, Pernambuco, Rio Grande do Sul, Santa Catarina, and São Paulo.

Culture	B soil concentration	Fertilizer recommendation
	mg kg^{-1}	kg ha^{-1}
Cotton	< 0.20 to > 0.60	2.5 to 1.0
Coffee	< 0.60 to > 1.00	4.0 to 1.0
Sugarcane	< 0.20 to > 0.60	2.0 to 0.0
Citrus	< 0.60	3.0 to 2.0
Soybean	for any level	1.0

Source: Cantarella et al. (2022).

have a substantial impact on crop yield, underscoring the necessity for precise micronutrient management (Franco et al., 2023; Mattos Junior et al., 2024). Similarly, studies have demonstrated that Mn toxicity can occur at relatively low levels in certain soil types (Skórka et al., 2023; Wang et al., 2023). These examples underscore the complexity of micronutrient management in agriculture and the need for careful consideration of soil and crop-specific factors in fertilization practices.

Boron levels that fall below the established limits should be interpreted as indicative of B deficiency. Conversely, levels exceeding the specified range's upper limit suggests B sufficiency but not an excess that would compromise productivity. Therefore, B fertilizer is strongly recommended for the predominant Brazilian crops (Table 3) (Cantarella et al., 2022).

Final remarks

The positive impact of B on plant growth is well-documented, particularly in contexts where the soil environment is characterized by optimal B levels. B's absorption and transport mechanisms from the soil to the roots and subsequently to the leaves are pivotal for understanding B's structural and hormonal significance and economic importance in tropical and subtropical agricultural regions. Moreover, B plays a crucial role in plant-pathogen interaction, enhancing plant resistance to diseases and pests. However, the effect of B on plants is subject to variation depending on the type of plant, stage of development, dose applied, and environmental conditions. Therefore, it is imperative to study the response of plants to B under different conditions to optimize the use of this micronutrient in agriculture.

Acknowledgments

The authors are grateful to the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), grant #2020/03271-9, grant #2022/08391-8, to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), grant number 311203/2021-3, and to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), finance code 001.

Authors' Contributions

Conceptualization: Abreu-Junior CH, Lavres Júnior J. **Data curation:** Abreu-Junior CH, Rocha JR, Barros THS, Moreira GR, Rezende VP, Cagliari VNS, Rocha Junior C, Coelho AD, Boaretto RM, Capra GF, Nogueira TAR, Jani AD, Lavres Júnior J. **Formal analysis:** Abreu-Junior CH, Rocha JR, Barros THS, Moreira GR, Rezende VP, Cagliari VNS, Rocha Junior C, Coelho AD, Boaretto RM, Capra GF, Nogueira TAR, Jani AD, Lavres Júnior J. **Investigation:** Abreu-Junior CH, Rocha JR, Barros THS, Moreira GR, Rezende VP, Cagliari VNS, Rocha Junior C, Coelho AD, Boaretto RM, Capra GF, Nogueira TAR, Jani AD, Lavres Júnior J. **Project administration:** Abreu-Junior CH, Rocha JR, Barros THS, Moreira GR, Boaretto RM, Lavres Júnior J. **Supervision:** Abreu-Junior CH, Rocha JR, Barros THS, Moreira GR, Boaretto RM, Lavres Júnior J. **Validation:** Abreu-Junior CH, Rocha JR, Barros THS, Moreira GR, Boaretto RM, Lavres Júnior J. **Writing – original draft:** Abreu-Junior CH, Rocha JR, Barros THS, Moreira GR, Rezende VP, Cagliari VNS, Rocha Junior C, Coelho AD, Boaretto RM, Lavres Júnior J. **Writing – review & editing:** Abreu-Junior CH, Rocha JR, Barros THS, Moreira GR, Rezende VP, Cagliari VNS, Rocha Junior C, Coelho AD, Boaretto RM, Capra GF, Nogueira TAR, Jani AD, Lavres Júnior J.

Conflict of interest

The authors declare no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

The information and database for this research are not currently on a platform or website. The corresponding author can provide them.

Declaration of use of AI Technologies

No AI Technologies were used to edit this manuscript.

References

Aasim M, Akgür Ö, Yıldırım B. 2022. An overview on boron and pollen germination, tube growth and development under in vitro and in vivo conditions. p. 293-310. In: Aftab T, Papadakis IE, Brown PH, Landi M, Araniti F. eds. Boron plants in agriculture: exploring the physiology of boron and its impact on plant growth. Elsevier, Amsterdam, The Netherlands. https://doi.org/10.1016/B978-0-323-90857-3.00014-X

Abreu CA, Abreu MF, van Raij B, Bataglia OC, Andrade JC. 1994. Extraction of boron from soil by microwave heating for ICP-AES determination. Communications in Soil Science and Plant Analysis 25: 3321-3333. https://doi.org/10.1080/00103629409369267

Abreu MF, Abreu CA, Andrade J. 2001. Determinação de boro em água quente, usando aquecimento com microonda. p. 231-239. In: van Raij B, Andrade JC, Cantarella H, Quaggio JA. eds. Análise química para avaliação da fertilidade de solos tropicais. Instituto Agronômico de Campinas, Campinas, SP, Brazil (in Portuguese).

Abreu CA, van Raij B, Abreu MF, González AP. 2005. Routine soil testing to monitor heavy metals and boron. Scientia Agricola 62: 564-571. https://doi.org/10.1590/S0103-90162005000600009

Aftab T, Landi M, Papadakis IE, Araniti F, Brown PH. 2022. Boron in Plants and Agriculture: Exploring the Physiology of Boron and its Impact on Plant Growth. Elsevier, Amsterdam, The Netherlands.

Antoniadis V, Chatzissavvidis C, Paparnakis A. 2013. Boron behavior in apple plants in acidic and limed soil. Journal of Plant Nutrition and Soil Science 176: 267-272. https://doi.org/10.1002/jpln.201100366

Aquea F, Federici F, Moscoso C, Vega A, Jullian P, Haseloff J, Arce-Johnson P. 2012. A molecular framework for the inhibition of *Arabidopsis* root growth in response to boron toxicity. Plant Cell Environment 35: 719-734. https://doi.org/10.1111/J.1365-3040.2011.02446.X

Ardic M, Sekmen AH, Turkan I, Tokur S, Ozdemir F. 2009. The effects of boron toxicity on root antioxidant systems of two chickpea (*Cicer arietinum* L.) cultivars. Plant and Soil 314: 99-108. https://doi.org/10.1007/s11104-008-9709-y

Arunkumar BR, Thippeshappa GN, Anjali MC, Prashanth KM. 2018. Boron: A critical micronutrient for crop growth and productivity. Journal of Pharmacognosy and Phytochemistry 7: 2738-2741.

Blevins DG, Lukaszewski KM. 1998. Boron in plant structure and function. Annual Review of Plant Biology 49: 481-500. https://doi.org/10.1146/annurev.arplant.49.1.481

Blevins DG. 2009. More hidden hunger: Special nutrient needs of plants based on their structure and function. UC Davis: Department of Plant Sciences, Davis, CA, USA.

Bolaños L, Abreu I, Bonilla I, Camacho-Cristóbal JJ, Reguera M. 2023. What can boron deficiency symptoms tell us about its function and regulation? Plants 12: 777. https://doi.org/10.3390/plants12040777

Botelho RV, Müller MML, Umburanas RC, Laconski JMO, Terra MM. 2022. Boron in fruit crops: plant physiology, deficiency, toxicity, and sources for fertilization. p. 29-50. In: Aftab T, Papadakis IE, Brown PH, Landi M, Araniti F. eds. Boron in plants and agriculture: exploring the physiology of boron and its impact on plant growth. Elsevier, Amsterdam, The Netherlands. https://doi.org/10.1016/B978-0-323-90857-3.00015-1

Brdar-Jokanovic M. 2020. Boron toxicity and deficiency in agricultural plants. International Journal of Molecular Sciences 21: 1424. https://doi.org/10.3390/IJMS21041424

Brown PH, Shelp BJ. 1997. Boron mobility in plants. Plant and Soil 193: 85-101. https://doi.org/10.1023/A:1004211925160

Brown PH, Bellaloui N, Wimmer MA, Bassil ES, Ruiz J, Hu H, et al. 2002. Boron in plant biology. Plant Biology 4: 205-223. https://doi.org/10.1055/s-2002-25740

Cantarella H, Quaggio JA, Mattos Junior D, Boaretto RM, van Raij B. 2022. Boletim, 100: Recomendações de adubação e calagem para o estado de São Paulo. Instituto Agronômico de Campinas, Campinas, SP, Brazil (in Portuguese).

Chatterjee C, Sinha P, Agarwala SC. 1990. Interactive effect of boron and phosphorus on growth and metabolism of maize grown in refined sand. Canadian Journal of Plant Science 70: 455-460. https://doi.org/10.4141/cjps90-053

Chaudhary DR, Shukla LM, Gupta A. 2005. Boron equilibria in soil: a review. Agricultural Reviews 26: 288-294.

Chaves FS, Nogueira ARA, Souza GB, Primavesi AC. 2006. Avaliação de procedimento de extração e determinação de boro em amostras de solo. Boletim de Pesquisa e Desenvolvimento 5: 41 (in Portuguese).

Choudhary S, Zehra A, Naeem M, Khan MMA, Aftab T. 2020. Effects of boron toxicity on growth, oxidative damage, antioxidant enzymes and essential oil fingerprinting in *Mentha arvensis* and *Cymbopogon flexuosus*. Chemical and Biological Technologies in Agriculture 7: 1-11. https://doi.org/10.1186/s40538-019-0175-y

Cordeiro LFS, Cordeiro CFS, Ferrari S. 2022. Cotton yield and boron dynamics affected by cover crops and boron fertilization in a tropical sandy soil. Field Crops Research 284: 108575. https://doi.org/10.1016/j.fcr.2022.108575

Coskun D, White PJ. 2023. Ion-uptake mechanisms of individual cells and roots: short-distance transport. p. 11-71. In: Rengel Z, Cakmak I, White PJ. eds. Marschner's mineral nutrition of plants. Academic Press, San Diego, CA, USA. https://doi.org/10.1016/B978-0-12-819773-8.00018-6

Cruz MCP, Nakamura AM, Ferreira ME. 1987. Boron adsorption by soil: effects of boron concentration and soil pH. Pesquisa Agropecuária Brasileira 22: 621-626 (in Portuguese, with abstract in English).

Das AK, Purkait A. 2020. Boron dynamics in soil: classification, sources, factors, fractions, and kinetics. Communications in Soil Science and Plant Analysis 51: 2778-2790. https://doi.org/10.1080/00103624.2020.1849261

Epstein E. 1972. The inorganic components of plants. p. 267-324. In: Epstein E, Bloom AJ. eds. Mineral nutrition of pants: principles and perspectives. John Wiley, New York, NY, USA.

Ferreira GA, Hippler FWR, Prado LAS, Rima JAH, Boaretto RM, Quaggio JA, et al. 2021. Boron modulates the plasma membrane H^+-ATPase activity affecting nutrient uptake of *Citrus* trees. Annals of Applied Biology 178: 293-303. https://doi.org/10.1111/aab.12630

Franco A, Buoso S, Zanin L, Pinton R, Tomasi N. 2023. Copper toxicity in maize: the severity of the stress is reduced depending on the applied Fe-chelating agent. Journal of Plant Growth Regulation 42: 1567-1581. https://doi.org/10.1007/S00344-022-10641-1

García-Hernández ER, López GIC. 2005. Structural cell wall proteins from five pollen species and their relationship with boron. Brazilian Journal of Plant Physiology 17: 375-381. https://doi.org/10.1590/S1677-04202005000400005

García-Sánchez F, Simón-Grao S, Martínez-Nicolás JJ, Alfosea-Simón M, Liu C, Chatzissavvidis C, et al. 2020. Multiple stresses occurring with boron toxicity and deficiency in plants. Journal of Hazardous Materials 397: 122713. https://doi.org/10.1016/j.jhazmat.2020.122713

Garg OK, Sharma AN, Kona GRSS. 1979. Effect of boron on the pollen vitality and yield of rice plants (*Oryza sativa* L. var. Jaya). Plant and Soil 52: 591-594. https://doi.org/10.1007/BF02277956

Gerendas J, Heeschen V, Kahl S, Ratcliffe RG, Rudolph H. 1997. An investigation of N Me[tacute]abolism and pH regulation in *Sphagnum* using *in vivo* nuclear magnetic resonance and stable isotope mass spectrometry. Isotopes in Environmental and Health Studies 33: 21-29. https://doi.org/10.1080/10256019808036355

Goldbach HE, Yu Q, Wingender R, Schulz M, Wimmer M, Findeklee P, et al. 2001. Rapid response reactions of roots to boron deprivation. Journal of Plant Nutrition and Soil Science 164: 173-181. https://doi.org/10.1002/1522-2624(200104)164:2<173::AID-JPLN173>3.0.CO;2-F

Goldberg S. 1997. Reactions of boron with soils. Plant and Soil 193: 35-48. https://doi.org/10.1023/A:1004203723343

González-Fontes A, Navarro-Gochicoa MT, Camacho-Cristóbal JJ, Herrera-Rodríguez MB, Quiles-Pando C, Rexach J. 2014. Is Ca^{2+} involved in the signal transduction pathway of boron deficiency? New hypotheses for sensing boron deprivation. Plant Science 217-218: 135-139. https://doi.org/10.1016/j.plantsci.2013.12.011

Günes A, Alpaslan M. 2000. Boron uptake and toxicity in maize genotypes in relation to boron and phosphorus supply. Journal of Plant Nutrition 23: 541-550. https://doi.org/10.1080/01904160009382038

Gupta UC. 1993. Boron and its role in crop protection. p. 53-85. In: Gupta UC. ed. Physiology and biochemistry of boron in plants. CRC Press, Boca Raton, FL, USA.

Han S, Chen LS, Jiang HX, Smith BR, Yang LT, Xie CY. 2008. Boron deficiency decreases growth and photosynthesis, and increases starch and hexoses in leaves of citrus seedlings. Journal of Plant Physiology 165: 1331-1341. https://doi.org/10.1016/j.jplph.2007.11.002

Hu H, Brown PH. 1997. Absorption of boron by plant roots. Plant and Soil 193: 49-58. https://doi.org/10.1023/A:1004255707413

Kaya C, Tuna AL, Dikilitas M, Ashraf M, Koskeroglu S, Guneri M. 2009. Supplementary phosphorus can alleviate boron toxicity in tomato. Scientia Horticulturae 121: 284-288. https://doi.org/10.1016/j.scienta.2009.02.011

Koshiba T, Kobayashi M, Matsuoka K, Fujiwara T, Matoh T. 2013. Boron nutrition of cultured tobacco BY-2 cells: rapid induction of metabolic dysfunction in cells deprived of boron as revealed by microarray analysis. Soil Science and Plant Nutrition 59: 189-194. https://doi.org/10.1080/00380768.2013.763383

Long Y, Peng J. 2023. Interaction between boron and other elements in plants. Genes 14: 130. https://doi.org/10.3390/genes14010130

Lukaszewski KM, Blevins DG. 1996. Root growth inhibition in boron-deficient or aluminum-stressed squash may be a result of impaired ascorbate metabolism. Plant Physiology 112: 1135-1140. https://doi.org/10.1104/pp.112.3.1135

Luo Z, Zhang L, Hu W, Wang Y, Tao J, Jia Y, et al. 2024. Excessive boron fertilization-induced toxicity is related to boron transport in field-grown pomelo trees. Frontiers in Plant Science 15: 1438664. https://doi.org/10.3389/fpls.2024.1438664

Malavolta E. 1980. Elementos de Nutrição Mineral de Plantas. Agronômica Ceres, São Paulo, SP, Brazil (in Portuguese).

Mantovani JPM, Calonego JC, Foloni JSS. 2013. Boron leaf application at different growth stages of peanut. Revista Ceres 60: 270-278 (in Portuguese, with abstract in English). https://doi.org/10.1590/S0034-737X2013000200017

Marschner P, Rengel Z. 2012. Mineral Nutrition of Higher Plants. 3ed. Elsevier, Amsterdam, The Netherlands.

Martínez-Cuenca MR, Martínez-Alcántara B, Quiñones A, Ruiz M, Iglesias DJ, Primo-Millo E, et al. 2015. Physiological and molecular responses to excess boron in *Citrus macrophylla* W. PLoS One 10: e0137941. https://doi.org/10.1371/journal.pone.0134372

Mattiello EM, Ruiz HA, Silva IR, Sarkis JES, Neves JCL, Pucci MM. 2009. Phloem mobility of Boron in two eucalypt clones. Revista Brasileira de Ciência do Solo 33: 1695-1704. https://doi.org/10.1590/S0100-06832009000600018

Mattos Junior D, Huber LN, Petená G, Bortoloti GA, Hippler FWR, Boaretto RM. 2024. Biochemical and anatomical aspects of copper deficiency induced by high nitrogen supply in Citrus. Plant and Soil 496: 193-204. https://doi.org/10.1007/s11104-023-05899-7

Mehran M, Ashraf M, Shahzad SM, Shakir MS, Azhar MT, Ahmad F, et al. 2023. Growth, yield and fiber quality characteristics of Bt and non-Bt cotton cultivars in response to boron nutrition. Journal of Cotton Research 6: 1. https://doi.org/10.1186/s42397-023-00138-x

Mesquita GL, Zambrosi FCB, Tanaka FAO, Boaretto RM, Quaggio JA, Ribeiro RV, et al. 2016. Anatomical and physiological responses of citrus trees to varying boron availability are dependent on rootstock. Frontiers in Plant Science 7: 179382. https://doi.org/10.3389/fpls.2016.00224

Miwa K, Takano J, Fujiwara T. 2008. Molecular mechanisms of boron transport in plants and its modification for plant growth improvement. Tanpakushitsu Kakusan Koso 53: 1173-1179

Miwa K, Fujiwara T. 2010. Boron transport in plants: co-ordinated regulation of transporters. Annals of Botany 105: 1103-1108. https://doi.org/10.1093/aob/mcq044

Moreira A, Castro C, Oliveira FA. 2010. Yield, boron concentration and evaluation of extractants in soils cultivated with soybean. Ciência e Agrotecnologia 34: 367-373 (in Portuguese, with abstract in English). https://doi.org/10.1590/s1413-70542010000200014

O'Neill MA, Ishii T, Albersheim P, Darvill AG. 2004. Rhamnogalacturonan. II. Structure and function of a borate cross-linked cell wall pectic polysaccharide. Annual Review of Plant Biology 55: 109-139. https://doi.org/10.1146/annurev.arplant.55.031903.141750

Peak D, Luther GW, Sparks DL. 2003. ATR-FTIR spectroscopic studies of boric acid adsorption on hydrous ferric oxide. Geochimica Cosmochimica Acta 67: 2551-2560. https://doi.org/10.1016/S0016-7037(03)00096-6

Prado RM. 2021. Boron. p. 175-190. In: Prado RM. ed. Mineral nutrition of tropical plants. Springer, Cham, Germany.

Reid RJ, Fitzpatrick KL. 2009. Redistribution of boron in leaves reduces boron toxicity. Plant Signaling & Behavior 4: 1091-1093. https://doi.org/10.4161/PSB.4.11.9798

Reid R. 2014. Understanding the boron transport network in plants. Plant and Soil 385: 1-13. https://doi.org/10.1007/s11104-014-2149-y

Riaz M, Kamran M, Aziz O, Wang X. 2022. Alleviation of boron toxicity in plants by silicon: mechanisms and approaches. p. 233-247. In: Aftab T, Papadakis IE, Brown PH, Landi M, Araniti F. eds. Boron plants in agriculture: exploring the physiology of boron and its impact on plant growth. Elsevier, Amsterdam, The Netherlands. https://doi.org/10.1016/B978-0-323-90857-3.00007-2

Rosolem CA, Quaggio JA, Silva NM. 2001. Algodão, Amendoim e Soja. p. 321-354. In: Ferreira ME, Cruz MCP, van Raij B, Abreu CA. eds. Micronutrientes e elementos tóxicos na agricultura. CNPq/FAPESP/POTAFOS, Jaboticabal, SP, Brazil (in Portuguese).

Rosolem CA, Leite VM. 2007. Coffee leaf and stem anatomy under boron deficiency. Revista Brasileira de Ciência do Solo 31: 477-483. https://doi.org/10.1590/S0100-06832007000300007

Santos HG, Carvalho Júnior W, Dart RO, Áglio MLD, Sousa JS, Pares JG, et al. 2011. O Novo Mapa de Solos do Brasil: legenda atualizada. Embrapa, Rio de Janeiro, RJ, Brazil (in Portuguese).

Sarafi E, Siomos A, Tsouvaltzis P, Chatzissavvidis C, Therios I. 2017. Boron toxicity effects on grafted and non-grafted pepper (*Capsicum annuum*) plants. Journal of Soil Science and Plant Nutrition 17: 441-460. https://doi.org/10.4067/S0718-95162017005000032

Schmidt MP, Siciliano SD, Peak D. 2021. The role of monodentate tetrahedral borate complexes in boric acid binding to a soil organic matter analogue. Chemosphere 276: 130150. https://doi.org/10.1016/j.chemosphere.2021.130150

Shabala L, Zhang J, Pottosin I, Bose J, Zhu M, Fuglsang AT, et al. 2016. Cell-type-specific H^+-ATPase activity in root tissues enables K+ retention and mediates acclimation of barley (*Hordeum vulgare*) to salinity stress. Plant Physiology 172: 2445-2458. https://doi.org/10.1104/pp.16.01347

Shorrocks VM. 1997. The occurrence and correction of boron deficiency. Plant and Soil 193: 121-148. https://doi.org/10.1023/A:1004216126069

Simón-Grao S, Nieves M, Martínez-Nicolás JJ, Cámara-Zapata JM, Alfosea-Simón M, García-Sánchez F. 2018. Response of three citrus genotypes used as rootstocks grown under boron excess conditions. Ecotoxicology and Environmental Safety 159: 10-19. https://doi.org/10.1016/j.ecoenv.2018.04.042

Skórka M, Sieprawska A, Telk A. 2023. The implication of manganese surplus on plant cell homeostasis: a review. Journal of Plant Growth Regulation 42: 1327-1341. https://doi.org/10.1007/S00344-022-10637-X

Soares MR, Alleoni LRF, Casagrande JC. 2005. Thermodynamic parameters for boron adsorption reaction on highly weathered tropical soils. Química Nova 28: 1014-1022 (in Portuguese, with abstract in English). https://doi.org/10.1590/S0100-40422005000600016

Soares MR, Casagrande JC, Alleoni LRF. 2008. Boron adsorption in acric soils as a function of pH variation. Revista Brasileira de Ciência do Solo 32: 111-120 (in Portuguese, with abstract in English). https://doi.org/10.1590/S0100-06832008000100011

Sousa DM, Lobato E. 2004. Cerrado: Correção do Solo e Adubação. Embrapa, Rio de Janeiro, RJ, Brazil (in Portuguese).

Souza LT, Carr NF, Lavres J, Mazzafera P, Favarin JL. 2022. Boron deficiency affects ATP hydrolysis of plasma membrane and nutrients uptake in coffee: consequences for plant growth. Journal of Plant Nutrition 45: 2123-2134. https://doi.org/10.1080/01904167.2022.2043371

Souza Junior JP, Prado RM, Campos CNS, Sousa Junior GS, Costa MG, Teixeira SP, et al. 2023. Silicon modulate the non-enzymatic antioxidant defence system and oxidative stress in a similar way as boron in boron-deficient cotton flowers. Plant Physiology and Biochemistry 197: 107594. h ttps://doi.org/10.1016/j.plaphy.2023.02.024

Strawn DG. 2021. Sorption mechanisms of chemicals in soils. Soil Systems 5: 13. https://doi.org/10.3390/soilsystems5010013

Takano J, Miwa K, Fujiwara T. 2008. Boron transport mechanisms: collaboration of channels and transporters. Trends in Plant Science 13: 451-457. https://doi.org/10.1016/j.tplants.2008.05.007

Takano J, Tanaka M. 2023. Boron-sensing mechanisms involved in boron transport regulation in plants. Journal of Plant Nutrition and Soil Science 29: 1-8. https://doi.org/10.1002/jpln.202300029

Tanaka M, Fujiwara T. 2008. Physiological roles and transport mechanisms of boron: perspectives from plants. Pflügers Archiv: European Journal of Physiology 456: 671-677. https://doi.org/10.1007/s00424-007-0370-8

Taylor GJ, Macfie SM. 1994. Modeling the potential for boron amelioration of aluminum toxicity using the Weibull function. Canadian Journal of Botany 72: 1187-1196. https://doi.org/10.1139/b94-145

van Raij B, Andrade JC, Cantarella H, Quaggio JA. 2001. Análise Química para Avaliação da Fertilidade de Solos Tropicais. Instituto Agronômico de Campinas, Campinas, SP, Brazil (in Portuguese).

Wang Y, Li J, Pan Y, Chen J, Liu Y. 2023. Metabolic responses to manganese toxicity in soybean roots and leaves. Plants 12: 3615. https://doi.org/10.3390/plants12203615

Wimmer MA, Eichert T. 2013. Review: mechanisms for boron deficiency-mediated changes in plant water relations. Plant Science 203-204: 25-32. https://doi.org/10.1016/j.plantsci.2012.12.012

Yermiyahu U, Keren R, Chen Y. 2001. Effect of composted organic matter on boron uptake by plants. Soil Science Society of America Journal 65: 1436-1441. https://doi.org/10.2136/sssaj2001.6551436x

Zhou GF, Peng SA, Liu YZ, Wei QJ, Han J, Islam MZ. 2014. The physiological and nutritional responses of seven different citrus rootstock seedlings to boron deficiency. Trees: Structure and Function 28: 295-307. https://doi.org/10.1007/S00468-013-0949-Y

Zhou GF, Zhang LP, Li BX, Sheng O, Wei QJ, Yao FX, et al. 2019. Genome-wide identification of long non-coding RNA in trifoliate orange (*Poncirus trifoliata* (L.) Raf) leaves in response to boron deficiency. International Journal of Molecular Sciences 20: 5419. https://doi.org/10.3390/ijms20215419

Zhu Y, Cai J, Hosmane NS, Zhang Y. 2022. Introduction: basic concept of boron and its physical and chemical properties. p. 1-57. In: Zhu Y, Hosmane NS. eds. Fundamentals and applications of boron chemistry. Elsevier, Amsterdam, The Netherlands. https://doi.org/10.1016/B978-0-12-822127-3.00003-X