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Derleme Makalesi / Review Article

A Comprehensive Review on Exploring the Mechanisms of Boron Toxicity in Plants

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Abstract

This review explores the multifaceted role of boron (B) in plant stress responses, emphasizing its mechanisms of action and agricultural relevance. Plants face numerous environmental stresses, including drought, salinity, and heavy metal toxicity, which significantly impact their growth and productivity. Recent research underscores the importance of micronutrients like B in mitigating these stresses. Boron is vital for various biological processes, including cell wall stability, cytoskeletal functions, and numerous metabolic pathways, affecting plant growth, flowering, and yield quality. However, managing B levels is challenging due to its narrow range between deficiency and toxicity. This review highlights B's interactions with macronutrients (nitrogen, calcium, phosphorus, and potassium) and micronutrients (zinc and manganese), revealing complex regulatory mechanisms that influence nutrient uptake, plant growth, and stress responses. Additionally, the review examines plants' responses to B toxicity, including mechanisms to reduce B uptake, the production of B-chelating compounds, and enhanced antioxidant systems to mitigate oxidative stress. By providing a comprehensive understanding of B's impact on plant health and productivity, this review aims to inform future research and practical approaches for optimizing B management in agriculture, contributing to sustainable crop production.

Keywords: Plant resilience, nutrient interactions, abiotic stress, crop productivity, plant adaptation

1. Introduction

Plants have evolved intricate mechanisms to enhance their resilience against environmental stresses. Among these stressors, factors such as drought, salinity, and heavy metal toxicity can significantly impact plant growth and productivity (Lamalakshmi Devi et al., 2017). In recent years, there has been increasing research interest in the importance of micronutrients, particularly boron (B), in plant stress responses (García-Sánchez et al., 2020; Bari et al., 2023). Boron plays critical roles in various biological processes in plants, exerting significant effects on plant health and adaptation, especially under stressful conditions. Within the cell wall, B forms complexes (RG-II-B) that stabilize the pectin network, influencing cell wall integrity and pore size. Research suggests B might also have functions within the cytoskeleton and membrane. But the influence of B extends far beyond structure. The B participates in various metabolic processes, including those for nucleic acids, sugars, protein synthesis, phosphorus utilization, and the metabolism of phenols, nitrogenous compounds, and hormones. These processes ultimately determine plant growth (vegetative and reproductive), flowering time, and harvest quality (Vera-Maldonado et al., 2024).

The optimal concentration of B in plant tissues generally ranges between 30 and 75 mg/kg. However, these levels can vary significantly depending on the specific plant species and their unique B requirements (Arunkumar et al., 2018). A recent study by Janaki et al. (2020) highlights B deficiency as the second most prevalent micronutrient deficiency in plants, following zinc. This widespread deficiency of B is primarily attributed to the neglect of B in conventional nutrient management practices. Dicotyledonous plants, especially cotton, sunflower and tomatoes have high demand for this micronutrient. Due to the immobility of B within plants, its availability is crucial at all stages of growth, especially during the development of fruits and seeds. This immobility means that a continuous supply of B is necessary to support the plant's developmental processes throughout its life cycle. When B is deficient in these plants, it can lead to various growth problems including reduced root development, withering of flower buds, poor pod formation, and significantly diminished seed yield or even sterility during the reproductive phase (Thakur et al., 2023).

Unlike many other nutrients, the window between deficiency and toxicity is narrow. This characteristic makes it challenging to maintain optimal B levels in the soil. An excess level of B can be equally detrimental, acting as a major abiotic stressor in many agricultural regions worldwide (Yıldız et al., 2022). High B levels can inhibit germination, restrict root growth development, cause chlorotic or necrotic patches on leaf margins and tips, but roots typically show no visible symptoms (Mousavi and Motesharezadeh 2020). The overall consequences of excess B primarily stem from its three main metabolic impacts. Boron interferes with cell division and development by binding to ribose, present both as a free sugar and within RNA. Additionally, it disrupts primary metabolism by binding to ribose in ATP or NAD(P)H. Moreover, boron reduces cytosolic pH, thereby influencing protein conformation and biosynthesis (Reid et al., 2004). In species capable of phloem re-translocation of B, symptoms include dead apical sprouts and lesions near stems and petioles. High B concentrations disrupt various physiological processes, such as reducing photosynthetic rates, increasing lipid peroxidation, and altering antioxidant enzyme activity (Hua et al., 2021).

This review aims to comprehensively examine the multifaceted role of B in plant stress responses, particularly focusing on its mechanisms of action and agricultural relevance. By delving into the interactions between B and other essential nutrients and exploring how plants mitigate B toxicity through various physiological and biochemical strategies, this review seeks to provide a holistic understanding of B's impact on plant health and productivity. Furthermore, it underscores the importance of balanced B nutrition in optimizing plant growth and resilience under environmental stresses. Through this exploration, the review aims to highlight critical areas for future research and practical approaches to enhance B management in agricultural systems, ultimately contributing to sustainable crop production.

2.Interaction of boron with macronutrients

Additionally, due to its multifaceted involvement in plant physiology and biochemistry, B plays a critical role in regulating the uptake and utilization of other essential mineral elements. This influence on nutrient homeostasis is crucial for optimal plant growth and development (Vera-Maldonado et al., 2024). The interaction between B and nitrogen (N) is complex and bidirectional, as N levels can potentially influence B uptake in plants, thereby affecting the overall efficiency of these processes. B can be crucial for N fixation and assimilation, particularly in legume species, influencing nodulation and essential protein synthesis (Koohkan et al., 2016). Dinh et al. (2021) stated that the interaction between N and B levels significantly influences B uptake and transport in canola plants, with ammonium-induced acidity leading to an upregulation of B transport mechanisms, particularly under low B supply conditions. Nitrate-induced alkalinization alters B distribution between roots and shoots, indicating that the N form in the nutrient solution affects B uptake and transport dynamics, highlighting the importance of considering both N and B levels for optimizing plant growth and nutrient uptake. In another study Bielski et al. (2020) demonstrated that N and B interaction significantly influenced winter triticale grain yield and yield components, highlighting the importance of their combined application for optimal productivity. While N fertilization played a crucial role in grain yield, B fertilization positively impacted yield structure, particularly ears number per 1 m^2.

Boron and calcium (Ca) engage in a dynamic partnership within the plant cell wall. Calcium strengthens B complexes, fostering both structural integrity and adaptability (Liu et al., 2019). This collaboration extends beyond the cell wall, as Ca can lessen B toxicity and influence gene expression related to Ca transport and signaling when B is deficient (Akhtar et al., 2022). A field study conducted by Galeriani et al. (2022) revealed that spraying soybeans with a combined Ca and B solution during flowering significantly boosted their ability to convert carbon dioxide into sugars within leaves. This enhanced sugar production fueled increased pod formation and ultimately led to higher grain yield. İlyas et al. (2021) conducted field experiments to investigate the impact of Ca, B, and their combination on autumn potato crop yield and quality. The results highlighted that while both 0.06% Ca and 0.04% B alone improved yield and quality parameters, the combined application of 0.06% Ca + 0.02% B during early planting in the first week of October yielded the most significant benefits, emphasizing the synergistic effects of using Ca and B together in enhancing potato yield and quality.

Boron can influence phosphorus (P) uptake and transport; when supplied together, they improve plant growth and photosynthetic rates (Paz-Ares et al., 2022). According to findings by Cakmak et al. (2023), boron deficiency exacerbates phosphorus deficiency, resulting in decreased phosphorus uptake. However, the application of boron can potentially alleviate this issue, as borates share certain physiological and biochemical similarities with phosphates (Hua et al., 2021). In addition, the interaction between B and P, including the modulation of H+-ATPase activity, enhances nutrient absorption and plant development, though the molecular mechanisms are not fully understood (Zhao et al., 2020). In a study conducted by Zhao et al (2021) showed that the interaction between B and P fertilizers significantly influences rapeseed yield and P use efficiency, emphasizing the importance of balanced B and P nutrition for optimal productivity. The study demonstrated that different combinations of B and P fertilizers affect both seed yield and P use efficiency, highlighting the need for careful management of these nutrients in rapeseed cultivation. Moreover, the application of B and P fertilizers impacts soil bacterial diversity and composition, suggesting potential opportunities for enhancing nutrient cycling and crop performance through soil management practices.

Potassium (K) and B are essential partners in plant physiology, acting as buffers to maintain healthy conductive tissues. While limited research exists, studies suggest a positive synergy between B and K, with combined application enhancing seed oil content, overall plant growth, and yield in crops (Akhtar et al., 2022; Bons and Sharma, 2023). Field trials showed that foliar application of both potassium sources and boron significantly increased potato tuber yield and quality. Potassium alone improved the number and weight of tubers, while boron boosted the total yield and size distribution, favoring larger tubers (Ewais et al., 2020). This beneficial effect is likely due to potassium's role in maintaining a balanced cellular environment. The specific interaction between B and K may be attributed to influence of B on K uptake and membrane permeability, while excess B can disrupt this balance and reduce K availability in some plant tissues (Samet et al., 2015).

3.Interaction of boron with micronutrients

The interaction between B and zinc (Zn) in plants affects metabolic processes and mineral composition, with Zn supplementation mitigating adverse effects of high B levels on plant growth. Additionally, gene expression studies suggest regulatory roles for specific genes like HKX1, MAKR6, and RING1B in response to B and Zn interaction, indicating involvement in hormone signaling and stress responses (Bhadra et al., 2023). In a two-year field study, Safdar et al. (2023) showed that sole and combined application of B and Zn significantly improved seed and oil yield, oil quality, and various physiological traits in oilseed rape under semi-arid conditions. The optimal B and Zn application rate for maximizing yield, oil quality, and physiological attributes in oilseed rape was reported as 2 kg ha^{-1} B and 8 kg ha^{-1} Zn. Studies combining B, Zn, and manganese (Mn) nutrition in various crops demonstrate their influence on polyphenol concentration, lignin synthesis, disease resistance, and overall plant growth, emphasizing the importance of balanced micronutrient application for optimal agricultural productivity. Furthermore, the intricate relationship between B and Zn in plant physiology is crucial for understanding their combined effects on growth, photosynthesis, and water relations. B deficiency or toxicity profoundly affects various metabolic processes, including cell wall structure and function, leading to impaired growth and reduced photosynthetic rates. Conversely, Zn, as an essential micronutrient, influences enzyme activity, membrane integrity, and ROS scavenging, mitigating the adverse effects of B stress on plant growth and physiological processes. The synergistic interaction between B and Zn underscores the further field studies to validate these findings in various crop species and soil conditions (Tavallali, 2017).

4. Plants's response to boron toxicity

Boron toxicity reduces crop yield and quality in numerous agricultural regions globally, often arising naturally in alkaline and saline soils where rainfall is low, and leaching is minimal. (Camacho-Cristóbal et al. 2018; Gokceoglu and Cimrin, 2022). The effects of B toxicity vary depending on a plant species' capability to re-translocate B within the phloem, with symptoms appearing first in older tissues in species where B is relatively immobile. Conversely, in species where B can be remobilized through the phloem sap, symptoms primarily manifest in actively growing tissues (Landi et al., 2019).

Boron tolerance in plants involves several key mechanisms: reducing B uptake by the root system and effluxing excess B from roots, changing in root morphology, stimulating the production of B-chelating organic compounds like polyalcohols and phenolics, bolstering the antioxidant system to counteract B-induced oxidative stress, and compartmentalizing B into less harmful organelles and sites within cells (Landi et al., 2019). Khan et al. (2023) used RNA sequencing to investigate the mechanisms behind boron tolerance in a previously unexplored wheat relative, *Triticum dicoccum* (PI94655). Their analysis revealed diverse pathways potentially involved in tolerance, including the regulation of transporters, changes in metabolic pathways, and the involvement of specific transcription factor families. This tolerant *T. dicoccum* genotype holds promise as a breeding resource for improving boron tolerance in modern wheat varieties. Additionally, the identified genes may be valuable tools for future studies on boron stress tolerance in wheat.

4.1. Protecting cellular functions: segregating b into organelles and specific locations

A wheat gene family (TaBOR) potentially regulates B uptake and distribution. Fourteen TaBOR genes with diverse tissue expression patterns and responsiveness to B levels have been identified by Wang et al. (2022). These genes reside on multiple chromosomes and possess promoter regions sensitive to light, hormones, and stress. Various crops and their varieties exhibit varying capacities to grow in high B soils. Varieties of wheat and barley tolerant to excess B have lower B concentrations in their tissues due to efficient B efflux transporters and reduced B entry channels (Martinez-Cuenca et al., 2015; Metwally et al., 2017). Tolerance mechanisms also involve morphological root changes and transcription factors that help maintain root growth. Tolerance to excess B in plants can be attributed to mechanisms such as morphological changes in roots, where increased reducing sugars help sustain root growth, and the involvement of transcription factors. However, variations in B tolerance among cultivars are not solely due to B accumulation in the leaves. Studies indicate that tolerant varieties may also have other physiological or genetic adaptations that contribute to their resilience. Some tolerant cultivars express Bor2-like genes, which transport B into vacuoles, reducing its toxicity and allowing higher accumulation without harming physiological processes (García-Sánchez et al., 2020).

In a recent study, Erkan and Akçay (2024) investigated miRNA's potential role in cotton's response to boron toxicity. They discovered that overexpressing miR408 enhanced cotton's tolerance to B stress, evidenced by reduced ion leakage and MDA levels, and increased proline, chlorophyll, and water content. Additionally, miR408 overexpression significantly impacted the expression of BOR1, BOR2, PIP1;1, and PIP2;1 aquaporins. These genes exhibited altered expression patterns under B toxicity compared to controls. While further research is needed, their study sheds light on cotton transporter genes and miR408's role in B stress. This suggests miR408 overexpression could be a promising strategy for enhancing plant tolerance to B stress and developing transgenic plants for B phytoremediation.

4.2. Production of boron chelating organic compounds

Under conditions of B toxicity, particularly prevalent in dry environments, plant performance and productivity are significantly impacted (Landi et al., 2019). A study conducted by Papadekis et al. (2018) on loquat seedlings exposed to varying B concentrations aimed to investigate how B affects sugar/polyol metabolism in polyol-producing tree species like loquat and how changes in leaf and stem anatomy may protect young tissues from B toxicity. The results revealed B accumulation primarily in top leaves, top bark, and top wood, with no alteration in allocation patterns between control and B-stressed plants. Excess B led to structural changes in top leaves, promoting the development of cork and collenchyma cells with increased cell wall thickness, possibly to sequester B in less harmful tissues. These findings suggest that while changes in sugar metabolism and anatomical adaptations partially aid young tissues in tolerating B stress, complete preservation is not achieved.

4.3. The role of antioxidants under boron toxicity

Excess B disrupts photosynthesis, impairing CO_2 uptake and causing structural damage to thylakoids, which leads to the production of ROS as unused electrons and light energy interact with molecular oxygen (Antonopoulou and Chatzissavvidis, 2022). The precise mechanisms of B tolerance remain elusive, but studies suggest that antioxidants and antioxidant enzymes may play a protective role. Antioxidants neutralize ROS, preventing damage to membranes, proteins, and nucleic acids. Plants use enzymatic and non-enzymatic antioxidant defense systems. Enzymatic defenses include superoxide dismutase (SOD), peroxidases (POX), catalase (CAT), and enzymes of the ascorbate-glutathione pathway. These enzymes work together to scavenge ROS and protect cells (Mittler, 2002). Plants with more robust antioxidant defense systems appear to exhibit greater tolerance to B stress (Landi et al., 2019). Ardıç et al. (2009) examined the oxidative stress and antioxidant response to B in chickpea cultivars with varying drought tolerance. The drought-tolerant cultivar showed increased shoot length at high B levels, while the drought-sensitive cultivar exhibited reduced shoot length and higher lipid peroxidation. Antioxidant enzyme activities (CAT, APX, and SOD) increased in drought-tolerant cultivar but not in drought-sensitive cultivar, suggesting a stronger antioxidative response in drought-tolerant cultivar. The researchers attributed to B tolerance to improved ability to scavenge reactive oxygen species and reduce lipid peroxidation.

The effects of B toxicity on rice seedlings have been investigated by Riaz et al. (2021). The researchers reported that excessive B levels inhibited root and shoot growth and caused visible stress on leaves, evidenced by reduced chlorophyll content. B toxicity led to oxidative stress and lipid peroxidation in cell membranes, with higher B concentrations accumulating more in leaves than roots. Over 80% of B was adsorbed onto the cell walls in both roots and leaves, and the free form of B was higher in treatments with elevated B levels. In addition, high B concentrations altered the functional groups in leaf cell walls. The study suggested that B-induced growth inhibition might be linked to increased B uptake in upper parts of the plant, oxidative damage, and variations in B forms, contributing to chlorosis.

Boron toxicity can be alleviated by Ca in various crops. In sweet pepper (*Capsicum annuum*), physiological and biochemical responses, such as the activation of antioxidant enzyme activities, have been initiated to counteract B toxicity (Piñero et al., 2017). Liu et al. (2021) investigated the mechanisms by which Ca alleviates B toxicity in trifoliate rootstock, crucial for citrus production. They examined various Ca levels alongside B concentrations to understand tolerance mechanisms. Results revealed that Ca (2.46 mM) significantly boosted root growth under B toxicity, enhancing root dry weight by 32.26% and fresh weight by 24.60%. While total B absorption remained unaffected, Ca reduced B's utilization efficiency in cell walls and stimulated antioxidant enzymes, mitigating reactive oxygen species. The effectiveness of Ca foliar sprays in mitigating excess B symptoms in pistachio rootstocks cultivated under saline conditions have been investigated by Rabari et al. (2023). Soluble Ca forms were applied as foliar sprays on three pistachio rootstocks irrigated with B-containing water. Excess B impeded growth and affected various parameters. However, foliar Ca sprays significantly reduced B accumulation in plant tissues, particularly in leaves, stems, and roots. Both Ca-Chelate and $CaCl_2$ treatments significantly improved growth and physiological responses, with Ca-Chelate showing superior effectiveness. The researchers reported that rootstock tolerance to B toxicity varied.

Ethylene signaling may play a key role in mediating physiological and metabolic changes in tomatoes under fluctuating B levels. The influence of ethylene signaling on tomato plants' responses to B deficiency and toxicity has been investigated by Pereira et al. (2023). They used tomato mutants with altered ethylene signaling pathways to investigate these connections. While B stress didn't necessarily inhibit plant growth, it significantly impacted functions like photosynthesis and chlorophyll production. Interestingly, B toxicity triggered visible damage on roots and leaves, coinciding with increased ethylene production in shoots. Furthermore, mutants with impaired ethylene signaling displayed greater sensitivity to B toxicity, showing reduced fruit production and altered plant development.

Ascorbic acid (AsA), a powerful plant antioxidant, plays a complex role in response to B toxicity. AsA directly scavenges reactive oxygen species (ROS) generated under B stress, protecting cellular components from damage. Abiotic stresses, including B toxicity, are known to trigger a higher accumulation of AsA compared to other stresses (Nawaz et al., 2023). Studies have demonstrated variable AsA levels in different plant species, cultivars, and under varying B stress conditions. While some plants exhibit increased AsA content under B toxicity, others show a decrease, suggesting a stress-specific response and potential dependence on the activity of other antioxidant enzymes like ascorbate peroxidase (APX). In a study by Landi et al. (2013), the purple-leaved 'Red Rubin' cultivar of sweet basil showed increased AsA levels and enhanced antioxidant capacity compared to the green-leaved 'Tigullio' cultivar, which displayed visible B toxicity symptoms. This suggests that AsA accumulation may be a protective mechanism against B-induced oxidative stress in certain plant species.

Glutathione (GSH), a potent plant antioxidant, plays a complex role in response to B toxicity. The potential of GSH to mitigate B toxicity by directly scavenging harmful ROS generated by excess B. However, research on the direct impact of B on GSH content presents a mixed picture, with some studies showing inhibition and others indicating an increase. Additionally, GSH's interplay with AsA in the plant's antioxidant response to B toxicity is complex, with a potential link between GSH and AsA levels. Overall, the relationship between B and GSH appears multifaceted, with GSH offering both detoxification benefits and being influenced by other factors (Landi et al., 2012). Kohnenharshi and Demir (2023) explored how glutathione (GSH) and proline can help wheat (*Triticum aestivum* cv.) resist B toxicity. Application of GSH alongside excess B improved root and shoot growth, chlorophyll content, and phenolic compounds compared to B alone. This suggests GSH helps mitigate the negative effects of B toxicity. Interestingly, both B toxicity and combined B+GSH treatments increased total GSH levels in wheat, although B+proline application actually decreased GSH content. Overall, the study suggested that both GSH and proline can act as antioxidants under B stress, reducing harmful molecules and boosting the activity of antioxidant enzymes. GSH appears to be generally more effective than proline in mitigating the detrimental effects of B toxicity.

Melatonin acts as a plant growth regulator, influencing various physiological processes like seed germination, root development, and flowering. Melatonin also plays a role in stress management, helping plants cope with environmental stressors like drought, salinity, and heavy metals (Khan et al., 2020). Al-Huqail et al. (2020) studied the role of melatonin in regulating wheat seedlings' carbohydrate and proline metabolism, photosynthesis, and antioxidant systems under B toxicity conditions. High B levels inhibited photosynthesis and led to oxidative damage in wheat seedlings by increasing malondialdehyde content and activity of oxidative enzymes. However, foliar application of melatonin improved photosynthetic pigments concentration, enhanced plant growth attributes, and increased nutrient uptake and enzymatic antioxidants even under non-toxic conditions. Melatonin effectively mitigated the adverse effects of excess B by enhancing plant defense mechanisms and reducing cellular oxidative damage.

5. Conclusions and Recommendations

5.1. Conclusions

This review explores the multifaceted role of boron (B) in plant responses to environmental stresses. It highlights the importance of maintaining optimal B levels for plant health and productivity. Boron plays a crucial role in plant stress responses, influencing various biological processes essential for plant health and adaptation. Its involvement in metabolic pathways, cell wall structure, and nutrient uptake underscores its significance in enhancing plant resilience against environmental stresses. However, maintaining optimal B levels in plants presents a challenge due to the narrow window between deficiency and toxicity. Excess B can lead to detrimental effects on plant growth and development, highlighting the importance of balanced B nutrition in agricultural practices.

5.2. Recommendations

Optimizing B Management: Implementing efficient B management practices is crucial to ensure optimal B levels in soils. This includes regular soil testing, targeted B fertilization based on crop requirements, and consideration of B mobility within plants.

Integrated Nutrient Management: Develop integrated nutrient management strategies that consider the interactions between B and other essential nutrients for optimal plant growth and stress tolerance. Incorporating B into integrated nutrient management strategies alongside other essential nutrients can enhance overall nutrient uptake and plant growth. This approach should consider the interactions between B and macronutrients/micronutrients to maximize agricultural productivity. Explore the potential of foliar applications of B combined with other nutrients like Ca to improve plant performance in B-deficient or B-toxic soils. Investigate the use of plant growth regulators like melatonin and stress protectants like glutathione as potential tools to mitigate B toxicity and enhance plant resilience.

Breeding for B Tolerance: Breeding programs should prioritize the development of crop varieties with enhanced tolerance to both B deficiency and toxicity. Identifying genetic markers associated with B tolerance can facilitate the breeding of resilient cultivars suited to varying soil B conditions.

Research on B-Responsive Genes: Further research is needed to elucidate the molecular mechanisms underlying B stress responses in plants. Identifying B-responsive genes and understanding their regulatory networks can provide valuable insights into enhancing plant tolerance to B-related stresses. In addition, foster collaboration between plant physiologists, soil scientists, and agricultural engineers to develop sustainable B management practices for various agricultural ecosystems.

Education and Outreach: Educating farmers and agricultural practitioners about the importance of B in plant nutrition and its role in stress tolerance is essential. Outreach programs can promote the adoption of best management practices to optimize B use efficiency and mitigate the adverse effects of B stress on crop production.

By implementing these recommendations, stakeholders can harness the potential of boron to improve agricultural productivity, enhance crop resilience, and ensure food security in the face of changing environmental conditions.

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