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Boron-zinc interaction in plant growth and reproduction: Advances and future directions

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Abstract

Boron (B) and Zinc (Zn) are two of eight essential micronutrients required for optimal plant growth, development and reproduction. Boron is extremely important for proper cell wall formation, maintaining membrane integrity, pollen development, carbohydrate transport within the plant, and many processes related to plant reproduction. Zinc is a vital part of many enzymes and proteins in a plant which facilitate, amongst other things, as photosynthesis, auxin production, protein metabolism, and antioxidative processes. When either of these two micronutrients is deficient in a plant, physiological and biochemical processes become severely disrupted, as evidenced by reduced crop productivity and overall fruit quality. Numerous published studies have reported that when B and Zn are applied in combination to a variety of crops, including: groundnuts, hazelnuts, walnuts, apples, potatoes, strawberries, olives, and many other types of field crops as well as many types of horticultural crops, plant growth and nutrient uptake are greatly increased, yield and yield component parameters and fruit quality parameters are likewise greatly increased. All of which are the result of the synergistic action of B and Zn, through improved photosynthetic efficiency and enzyme activity, improved pollen germination and fruit set, seed development, and improved antioxidant defense mechanisms. Collectively, the combined beneficial effects of the synergistic application of boron and zinc will maximize reproductive success, increase biomass accumulation, and enhance product quality to provide producers with a superior final product. This review highlights recent advances in understanding the interaction between boron and zinc, with a primary focus on the physiological, biochemical, reproductive, and molecular interactions of these two nutrients in plants. In particular, the authors discuss nutrient crosstalk, transport mechanisms, gene regulation, and their combined effect on improving stress resistance and efficiency of use of nutrients. The overall goal of the study is to consolidate present knowledge about how boron and zinc act together and suggest future research directions that could improve micronutrient management and therefore crop productivity, nutritional; quality, and various types of agricultural production practices.

Keywords: Boron, Pollen viability, Membrane integrity, Reproductive development, Zinc.

Introduction

Plants that grow in calcareous or alkaline soils with concurrent deficiencies of B and Zn to flourish, the interaction of B and Zn in plants is of vital importance for proper management of micronutrients. Studies typically focus on one or the other, but the combination of B and Zn has a significant effect on plant growth, plant yield, plant quality and plant reproductive development. Both micronutrients are involved in the physiological and biochemical processes of plant growth, development, reproduction, and countless other physiological and biochemical processes. This review article is specifically focused on boron and zinc which is two of the important essential micronutrients (Fe, B, Zn, Ni, Mn, Cu, Mo, and Cl) required for plant survival. The two essential micronutrients, i.e. B and Zn, are critical to the regulation of many metabolic and structural processes, thus promoting normal plant growth and development. Zinc and boron are essential micronutrients that regulate critical metabolic and structural processes, thereby ensuring normal plant growth and development (Papadakis *et al.*, 2018) [14]. They significantly influence flowering, pollen viability, pollination efficiency, and fruit set, thereby directly affecting reproductive success (Quddus *et al.*, 2018) [17]. In addition, both micronutrients contribute to antioxidant defense mechanisms, membrane stability, enzyme activation, and hormonal balance. Zinc plays a pivotal role in protein synthesis and auxin metabolism (Dubey & Pathak, 2024) [4], while boron is essential for cell wall formation, sugar transport, and reproductive tissue development (Pandey *et al.*, 2009) [12]. Moreover, their role in oil biosynthesis and overall yield enhancement highlights their agronomic significance. Considering their substantial impact on both vegetative and reproductive growth, Zn and B warrant special emphasis in micronutrient management strategies for sustainable crop production. Zinc is an essential micronutrient required for the proper functioning of over 300 enzymes (Gupta *et al.*, 2016) [6]. These include key enzymes such as alkaline phosphatase, superoxide dismutase (SOD), phospholipase, and alcohol dehydrogenase, among others. Most plants require zinc in concentrations ranging from 30 to 200 µg per gram of dry weight. In plants Zn has a pivotal role, in the metabolism of RNA, at the end which directly drives functions such as the creation of carbohydrates, proteins, and DNA. Additionally encourages blossoming and other phenomena associated to it. There is a meaningful physiological and molecular link between tryptophan biosynthesis, Zn and pollen tube formation, especially in the context of plant reproduction (Pandey *et al.*, 2013; Saadati *et al.*, 2016) [13,19]. Zinc functions at the molecular level mainly through zinc-finger proteins, which act as transcription factors controlling gene expression during flower development. The activation of a zinc finger motif is primarily due to the zinc ion (Zn^{2+}) itself.

Boron, an essential micronutrient, is crucial for cell membrane stability and is involved in cell wall biosynthesis, structural integrity, and cell division processes in plants. It also regulates sugar transport, contributes to the synthesis of plant hormones, and is involved in RNA metabolism, respiration, and various other physiological processes in plants (Saadati *et al.,* 2016) [19]. The level of boron in irrigation water depends on how well different crops can handle it. For example, crops that are sensitive to boron levels (such as pearl millet, bean, walnut, and peach) only tolerate low levels of boron (0.3 mg/L – 1.0 mg/L). Crops that have moderate tolerance to boron (such as oats, maize, barley, wheat, olives, sweet potatoes, potatoes, cotton, tomatoes, and pumpkins) can handle more of it, between 1.0 mg/L - 2.0mg/L. Finally, tolerant crops like sugar beet, date palm, carrot, lettuce, onion and asparagus would be the most tolerant and could handle the highest levels of boron (2.0mg/L - 4.0mg/L). Under neutral soil conditions boron will mainly exist as boric acid; however, plants need more boron for their reproductive period than during their vegetative period because boron increases flower production, flower retention and elongation of the pollen tube (Saadati *et al.,* 2016) [19]. The interaction between nutrients plays an important role in plant nutrition. The relationship between Zn and B is critical in determining the mineral content of calcareous soils; either positively or negatively affected were various minerals taken up or utilized in plants metabolic aging processes. Assessment of the effects of Zn and B application on Zea mays indicates that the effects of varying levels of boron decrease the height and dry weights of the plant's height. Furthermore, Zn has been shown to increase plant height and yield parameters significantly. This represents an antagonistic interaction regarding concentration but a synergistic interaction concerning promotion of growth with B and Zn; therefore, agronomically, zinc fertilization should be recommended in high-boron-containing soils or low-zinc-availability soils. However, the amount of change is often not sufficient to alter plant growth or yield, indicating that improved application techniques are required to increase low nutrient recovery. Tavallali, (2017) [22] indicates significant effects of both Zn and B on the physiological and biochemical responses of pistachio trees, through a synergistic interaction that increases photosynthetic activity, chlorophyll production, enzyme activity, and total plant growth within pistachio trees. Additionally, the relationship between both excessive and deficient levels of B adversely effects plant growth and photosynthesis under conditions of Zn deficiency. The study further reported that both excessive and deficient B levels adversely affect growth and photosynthetic performance, particularly under Zn-deficient conditions.

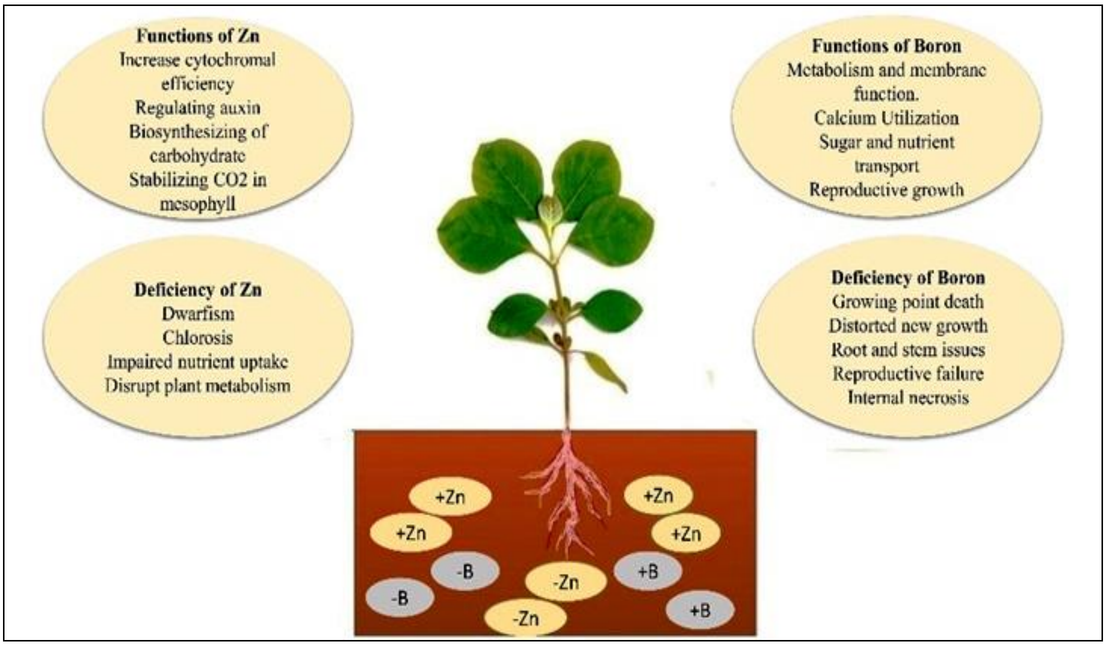

Fig 1: Conceptual illustration of Zn and B dynamics in plant systems.

Zinc functions in plants development and reproduction

Zinc is an essential micronutrient required for the normal growth and reproduction of plants. Although needed in small amounts, it plays a crucial role in maintaining the structural and functional integrity of cellular membranes and supports numerous vital physiological processes. Zinc is involved in plant growth regulation, enzyme activation, gene expression and regulation, phytohormone activity, protein synthesis, photosynthesis, carbohydrate metabolism, fertility, seed production, and disease resistance.

Zinc plays an important role in carbohydrate metabolism due to its influence on sugar transformation and photosynthesis. Zinc deficiency reduces photosynthetic activity by decreasing carbonic anhydrase activity (Pandey *et al.,* 2002) [11], impairing chloroplast photochemical processes, reducing chlorophyll content, and altering chloroplast structure. The maintenance of the integrity and usefulness of genetic information is the pivotalrole of zinc in the synthesis of proteins. Zn is necessary for the metabolism of proteins, and its involvement in this process is critical. Zinc is crucial for the structure of chromatin, metabolism of RNA and DNA, and the expression of the genes. Zinc deficiency leads to RNA degradation, reduced RNA polymerase activity, decreased ribosome numbers, and structural deformation of ribosomes, ultimately resulting in reduced protein synthesis.

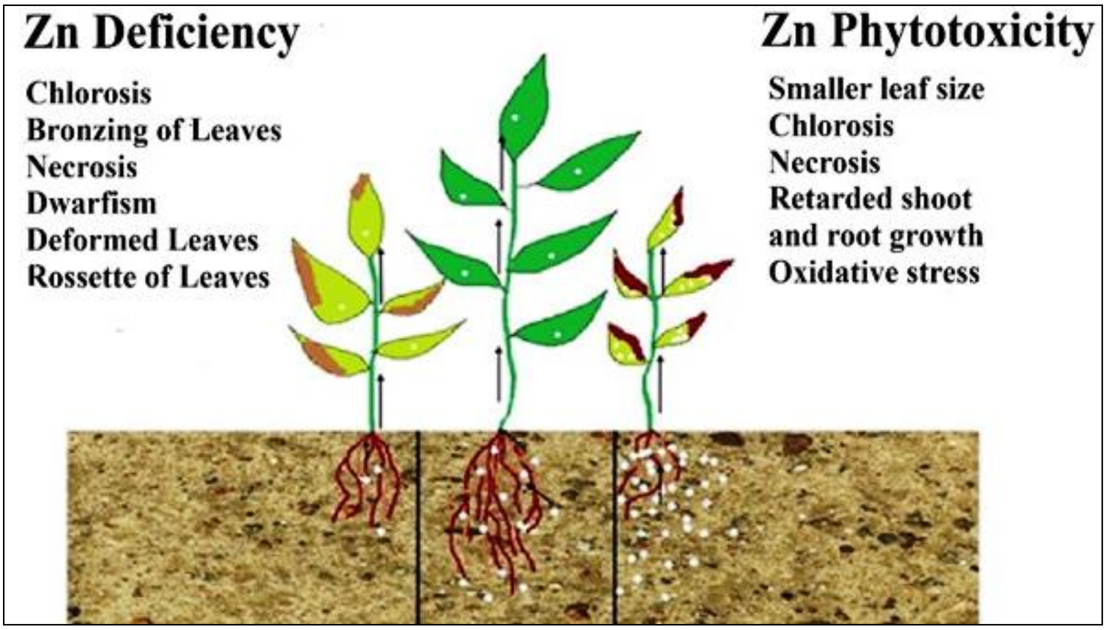

Fig 2: Conceptual illustration showing the effects of Zn deficiency and Phytotoxity on plant growth and development

Zinc toxicity symptoms in plants

The reduction in germination rate, biomass, and vigour are important physiological responses of plants to Zn toxicity, ultimately leading to reduced product quality and lower yield (Zhang *et al.*, 2017) [24]. According to Glinska *et al.*, (2016), [5] excessive zinc influences plant leaves with respect to both their number and area. This effect may be the consequence of either retardation in cell division or retardation of elongation, or may be due to both of these activities (Sofo *et al.*, 2018) [20]. Furthermore, elevated zinc concentrations cause damage to the structure of mitochondria of the tea plant, which in turn leads to a fall in the amounts of nicotinamide, which is a B-group vitamin. This, in turn, speeds up the breakdown of NAD+, which in turn slows down the metabolism of energy (Keunen *et al.*, 2011) [8]. This may be the reason why the overall plant development is slower. Zinc stress causes the leaves and/or shoots of plants (*viz. Arabidopsis*, Coriander, and Lettuce) to become red. This reddening may be attributed to higher levels of anthocyanins, which validates the fact that formation of phenolic compounds is due to stress response stimulated by Zn. Stoláriková-Vaculíková *et al.*, (2015) [21] reported that Zn toxicity in several plant species is characterized by rotting and blackening of root tips, along with reductions in root surface area, length, volume, and diameter.

Boron functions in plants

Boron is an essential component involved in several metabolically important processes in plants. Some other important roles of boron include its effects on the reproductive phase of growth and plant development, activation of reproductive structures, enhancement of seed quality (Perica *et al.,* 2001) [16], and regulation of the synthesis of certain metabolically important compounds such as polyphenols and antioxidants. Additionally, recent studies indicate that boron plays a vital role in nucleic acid biosynthesis, metabolism of phenolic compounds, carbohydrate synthesis and translocation, IAA oxidase formation, pollen tube development, and root elongation.

Boron deficiency effects in plants

Deficiency symptoms were immediately evident in plants that received no boron. The effects were particularly noticeable in the roots, which were stunted and produced numerous short lateral roots. The leaves developed a leathery texture and occasionally showed a deep crimson coloration, although this characteristic was not consistently observed. Despite the death of the apical growing points, new shoots continued to emerge for short periods (Marschner, 2012) [9]. However, boron-deficient plants consistently produced lower yields and developed fewer and smaller leaves compared to plants supplied with boron at any concentration. Boron deficiency reduces flower production by decreasing branching and impairing floral differentiation. Boron deficiency inhibits cell division, leading to a significant reduction in crop growth. As boron supply increases, yield improves up to an optimum level, beyond which further addition causes toxicity and reduces yield. If circumstances of deficiency or toxicity are present, then the yield of agricultural crops, whether in terms of vegetative or seed, will be reliant upon the available boron supply (Brdar-Jokanović, 2020) [2]. This is the case regardless of whether the crops are intended for vegetative or seed production. At levels of boron supply that are intermediate, the development of plants will not be influenced in any kind.

Efficient Boron Efflux (Exclusion Mechanism)

Boron tolerance in plants refers to the ability of some species or genotypes to survive and grow under high boron concentrations without suffering toxicity symptoms. This tolerance is governed by several physiological, biochemical, and genetic mechanisms. Resistance to boron (B) toxicity helps plants maintain their normal physiological and biochemical functions by sustaining proper growth and development, preserving photosynthetic efficiency, maintaining cell wall integrity and membrane stability, ensuring balanced nutrient uptake and utilization, supporting reproductive processes such as flowering and seed set, and preventing metabolic disruptions as well as oxidative damage.

Effect of Combined Application of Zn and B on Plant Growth, Yield, and Yield Attributes

The combined application of Zn and B plays a vital role in improving plant growth, productivity, and quality. Both micronutrients are essential for various physiological and biochemical processes, and their interaction often produces synergistic effects. Combined application of Zn and B has been found to positively influence plant growth and yield, resulting in improved development and enhanced physical quality of plants and fruits. It has been observed that foliar treatment of combined zinc and boron at concentrations of 0.4% and 0.15%, respectively, resulted in improved growth and production in tomato plants in contrast to control plants. In oilseed rape (*Brassica napus* L.), Safdar *et al*. observed beneficial effects comparable to those obtained from the integrated application of zinc and boron. Their soil application increased plant height by 10–13%, siliques per plant by 25–29%, and seeds per silique by 38–52% compared to the control. Additionally, oil yield increased by 53–54% over the control. In a similar vein, Saadati *et al.*, (2013) [18] presented their results for olive. In respect to the plants of control group, the size and the weight of fruits were seen to be increased when foliar treatments of combined zinc and boron were applied.

Response of Fruit Nutrient Concentration and Leaf Chlorophyll Content to Combined Zinc and Boron Application

Foliar application of micronutrient fertilizers significantly enhances the concentration of essential micronutrients in both leaves and fruits, as observed in crops such as oranges, olives, and apples. It is also reported that $ZnSO_4$ application increased zinc concentration in pomegranate leaves and fruit juice. Because Zn and B fertilizers are sprayed topically to leaves, the increased amount of Zn, B and Cu in the fruits is correlated with their higher amount in the leaves. These findings suggest that micronutrients may have been translocated via the phloem to regions with high metabolic activity (Pandey *et al.*, (2009). [12]

Effect of Zn and B on Fruit Physical Qualities

According to some reports, fruit yield of pomegranate and qualities of fruits, such as setting of fruit and their number per tree, were also improved by the combine use of zinc and boron and nearly identical results were also observed in cherry, olive, and papaya. Role that boron plays in the development of pollen grains, pollen tube prolongation and setting of fruits, as well as in other processes of metabolic importance like transportation of carbohydrate, is likely the reason behind the enhanced yield in pomegranate that results from foliar application of boron. Additionally, zinc hasan essential role in the tryptophan biosynthesis, and transfers metabolites either in the region of development of bud or to the bud itself. Zn also has an important function in flowering and in the initiation of fruit bud. $ZnSO_4$ and H_3BO_3 applied topically improved the average weight of fruit and percentage of juice in mandarins. This was attributed to zinc's role in tryptophan synthesis, which influences cell division and elongation.

Effect of Zn and B combine application on fruit's biochemical properties

The concentration of ascorbic acid in fruits was considerably raised by the integrateduse of Zn and vitamin B. Foliar spraying of zinc, either used singly or combined with B, prominently raised, in the juice of fruit, the concentration of sugars which are non-reducing in natureat the same time dramatically lowering the concentration of total sugar and thereducing sugar in fruit. Application of Zn and B, either individually or in combination, significantly enhances the total phenol content in apple juice, increasing it by 5.00–7.24%. Spraying Zn and B fertilizers also significantly stimulated the amount of anthocyanin pigments in fruit juice. Compared to B, Zn had a significantly stronger influence on the concentration of anthocyanins.

Effect of Zn and B combine application on content of oil in seeds

Zn and B fertilizer foliar sprays, when combined, greatly improve seed oil recovery during fruit development. According to Saadati *et al.*, (2013) [18], olive fruits' oil content was increased by foliar spraying them with zinc sulphate, boric acid, and their combination. These findings may indicate how zinc and boron affect the structural and mechanisms underlying the activity of enzymes in plant cells.

Effect of Zn and B combine application on nodulation

Zn and Bcombine application leads to the production ofmorenodules per plant in caseof field pea. In the stages from early to mid-flowering, the highest numbers of nodules formation have been observed. Afterwards, flowering, leads to reduced efficiency of root nodules and ultimately shutting down their production. Application of B at moderate concentration ensures positive effect on the nodulation capacity and fixation of nitrogen in legumes. Zn has a crucial function in metabolismand it is also associated in the activities like N-fixation by the formation of nodule. From various studies it has been also noticedthat combineapplications of Zn and B prove to be more efficient for theformationof nodule in comparison to applying them alone.

Effects of Combined Application of Zinc and Boron on Plant Growth and Development

Combined application of zinc and boron has been observed to enhance the concentrations of protein, sugars, and chlorophyll in the leaves of many plants. It has been reported that the combined application of zinc and boron significantly increases the protein, soluble sugar, and chlorophyll content in the leaves of oilseed rape (*Brassica napus* L.) compared to the control treatment. According to their findings Quddus *et al.*, (2018) [17], the application of zinc and boron in combination resulted in a greater protein content in field pea (*Pisum sativum* L.) as compared to control plants.

Discussion

Taken together, the conclusive findings herein indicate that zinc and boron are beneficial together or separately increasing plant growth, yield, and reproduction and all physiological and biochemical processes (Marschner, 2012) [9]. Additionally, according to Hafeez *et al.*, (2013) [7] the application of both zinc and boron results in superior performance than either property if used individually, since both micronutrients are involved in the transfer of photosynthates which, in turn, affects the quality and yield of both seeds and fruits. The present study indicate the adverse effect of micronutrient deficiency on cell wall formation, enzyme activation, photosynthesis, or reproductive success are limiting factors in reducing yield and quality of crops (Broadley *et al.*, 2007) [3]. The review highlights one of the major outcomes of using zinc and boron together is the synergistic effect of boron and zinc in enhancing nutrient uptake efficiency and improving the balance of plant nutrition. Carbohydrates are moved within the plant through boron and develop the reproductive portion while zinc aids in activating enzymes for protein synthesis and regulating hormones auxin biosynthesis (Barker & Pilbeam 2015) [1]. The synergistic activities of zinc and boron also enhance photosynthetic efficiency, membrane stability, and antioxidant systems, enhancing the plant's durability under good or stressed growing conditions. The review has found that maintaining balances among nutrients and at molecular levels is dependent on the integration of these two processes (nutrients). Transporters that transport boron and zinc into cells and throughout plants, and mechanisms for managing their expression, are critical to maintaining balance (homeostasis) of flowering plants, either as crops or wild plants (White, 2012) [23]. Overall, successful fertilization of flowering plants, improved seed development, development of fruit after flowering, are immense to final yield/quality (Onuh & Miwa 2021) [11]. A wide range of crops have exhibited positive responses to combined applications of boron and zinc, indicating this practice to be applicable across multiple crop species. However, the response of each species to the combined applications of the nutrients will vary according to the characteristics of the respective plant species; for example, in soils vs on skins, there would be different levels of nutrient availability. Thus, locally specific methods of nutrient management are critical for attaining maximum benefits.

Conclusion

Boron and zinc are two essential micronutrients that interact synergistically to regulate the growth, development, and reproductive processes of plants. The combined application of these nutrients is a promising method to enhance physiological efficiency, reproductive success, crop productivity, and the quality of the crops produced. In addition, integrated management of boron and zinc can contribute to sustainable agricultural production through improving nutrient use efficiency and increasing crop performance across varying agro-climatic conditions. The synergistic interaction of these two nutrients improves plant performance under normal growing conditions and helps improve the plants' tolerance to stresses caused by abiotic factors through the improvement of antioxidant defense mechanisms and regulation of metabolic activities. Although much progress has been made in this area, more research is needed to further understand the molecular mechanisms that govern the interaction between boron and zinc, optimize methods for applying both nutrients, and validate their effectiveness across a range of field environments. Future research should focus on precision management of nutrient application, methods for biofortifying crops, and sustainable fertilization methods to maximize nutrient use efficiency while sustaining agricultural productivity over time. The combined use of these two micronutrients will greatly contribute to sustainable agriculture, promote food security, and improve the nutritional quality of food consumed by humans.

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