



Functions of boron in plant roots: Current insights

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ABSTRACT

One of the most important components in achieving increased crop productivity is a balanced supply of necessary macro- and micronutrients. Among the various nutrients Boron (B) is recognised as a vital nutrient for the plant's life. However, inadequate availability of B can affect root development, nitrogen absorption, the integrity and function of cell walls and ultimately reduce the crop yield. Over 90 % of B in plants is found in cell wall, signifying its relevance in the growth and development of the root system. Since B is crucial for indispensable plant processes, it is a necessary constituent of rhamnogalacturonan II (RG-II), acting as a binding component in the cell wall, and as a result, it maintains membrane integrity, the indole acetic acid pathway, and cell wall synthesis. Therefore, this review aimed to assemble the novel information's of the function of boron in roots of the plant, deficiency symptoms, and the mechanisms of abiotic stresses management etc.

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1. Introduction

Since the beginning of plant life on earth, micro and macro nutrient have played a very significant role for the survival of plants life under continuous changing climatic conditions. Among the various micro and macronutrients, boron (B) has been recognised as one of the most important nutrients which contributes not only to the structural support of plants as well as give functional integrity in various metabolic processes (Pereira et al., 2021a, 2021b; Li et al., 2022; Sheng et al., 2024; Vera-Maldonado et al., 2024). More than 100 years ago, the crucial function of Boron for the growth, and development of plants was first identified (Warington, 1923). Nevertheless, expanding evidence indicates that Boron is also a necessary component in eukaryotes, such as humans (Nielsen, 2000). Further, at low concentrations, it is a crucial micronutrient for the regular operation of numerous organisms (Hussain et al., 2017) and enzymes like nitrogenase (Bonilla et al., 1990); however,

excess B can be harmful and can create several hurdles to sustain the smooth life cycle of plants (Rees et al., 2013). In addition, due to B toxicity, plants exhibit osmotic imbalances, necrosis, and chlorosis at the margin of leaves, completely leading to the cessation of crops (Turker et al., 2016; Arredondo and Bonomelli, 2023). B is recognised as a crucial ingredient for plant development and lack of boron (B) reduces agricultural yield globally, resulting in considerable economic losses, (Shorrocks, 1997; Graham 2008; Tanaka and Fujiwara, 2008; Kohli et al., 2023). Fertilizers have been used to resolve a B deficiency; however, on the other hand the widespread use of B in industrial products and agricultural chemicals has led to significant environmental issues (Yildirim and Kasim 2018). Furthermore, each year the soil accumulates around 500 million tonnes of fly ash near coal mines (Chen et al., 2017), leading to a significant release of B into the environment (Kara 2015). For crops, B is a crucial nutrient however the quantities needed are minimal, yet they can vary up to a point depending on the cultivar or variation of the plant and its species. Boron is often found in large amounts in the reproductive tissues and in the leaves (Marschner 2012). In general, greater contents may be found in legumes and tubers, which are then followed by fruit, vegetables, and cereals (Marschner 2012).

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Several metabolic and physiological processes in plants are impacted by low B availability, including shoot and root development, gene expression, phenolic and nitrogen metabolism, structure and function of the plasma membrane/cell wall, oxidative stress, and secondary metabolism (Camacho-Cristóbal et al., 2008a, 2008b; Herrera-Rodríguez et al., 2010; Camacho-Cristóbal et al., 2011). Three different mechanisms, each dependent on the level of B present in the soil, are used by root cells to absorb B as boric acid and load it to the xylem: (i) facilitated diffusion accomplished by nodulin-intrinsic proteins (NIPs) channels, (ii) passive diffusion via plasma membrane, and (iii) an energy dependent high affinity transport is enhanced by low B accessibility and mediated by BOR-transporters (Brown et al., 2002; Takano et al., 2008; Miwa and Fujiwara 2010; Reid 2014). Numerous biological activities of B in plants have been hypothesized, in addition to the structural significance of B as an assembly component in the cell wall, including membrane stabilization (Ferrol et al., 1993; Bolaños et al., 2004; Wimmer et al., 2009; Voxeur et al., 2014; Figs.1& 2) and its role in the functioning of plant cell metabolism (Brown et al., 2002; Camacho-Cristóbal et al., 2008a, 2008b; Wimmer et al., 2019). On the other hand, the signalling and regulatory systems governing the B stress response in crops are currently still very little recognized (Poza-Viejo et al., 2008). In plants, B deprivation symptoms include a sharp reduction in primary root development,

changed root morphology with an increase in root swelling, disorganization of the root apical meristem (RAM), and root hairs (hairy phenotype) (Dell et al., 1997; Archana and Verma 2017, Fig. 1). In *Arabidopsis thaliana*, continuous root growth and development are sustained by the root apical meristem, a reservoir of undifferentiated cells that give rise to the adult root architecture (Perilli et al., 2012; Sakamoto et al., 2019). Hormone signalling and transcriptional networks control these processes, and their actions as a result act to direct plant growth (Moubayidin et al., 2010, 2013; Takatsuka 2014; Jung and McCouch 2013; González-García et al., 2011). Boron can impart meristematic development in plants which is linked with plant developmental phase transition. Plants can defend themselves against B-toxicity after acquiring a sufficient amount of B from the soil (Pereira et al., 2021a, 2021b). Taking into the account of significant role of B in plants this review article is aimed to collect the recent developments to fulfill the gap of knowledge and to explore the future possibilities of B research in the field of plant science mainly in respect of three major aspect this is deficiency, toxicity and beneficial role.

1.1. Boron and roots: development to defense

Among vascular plants, roots and root-like structures have evolved several times independently (i.e., in lycopods twice and

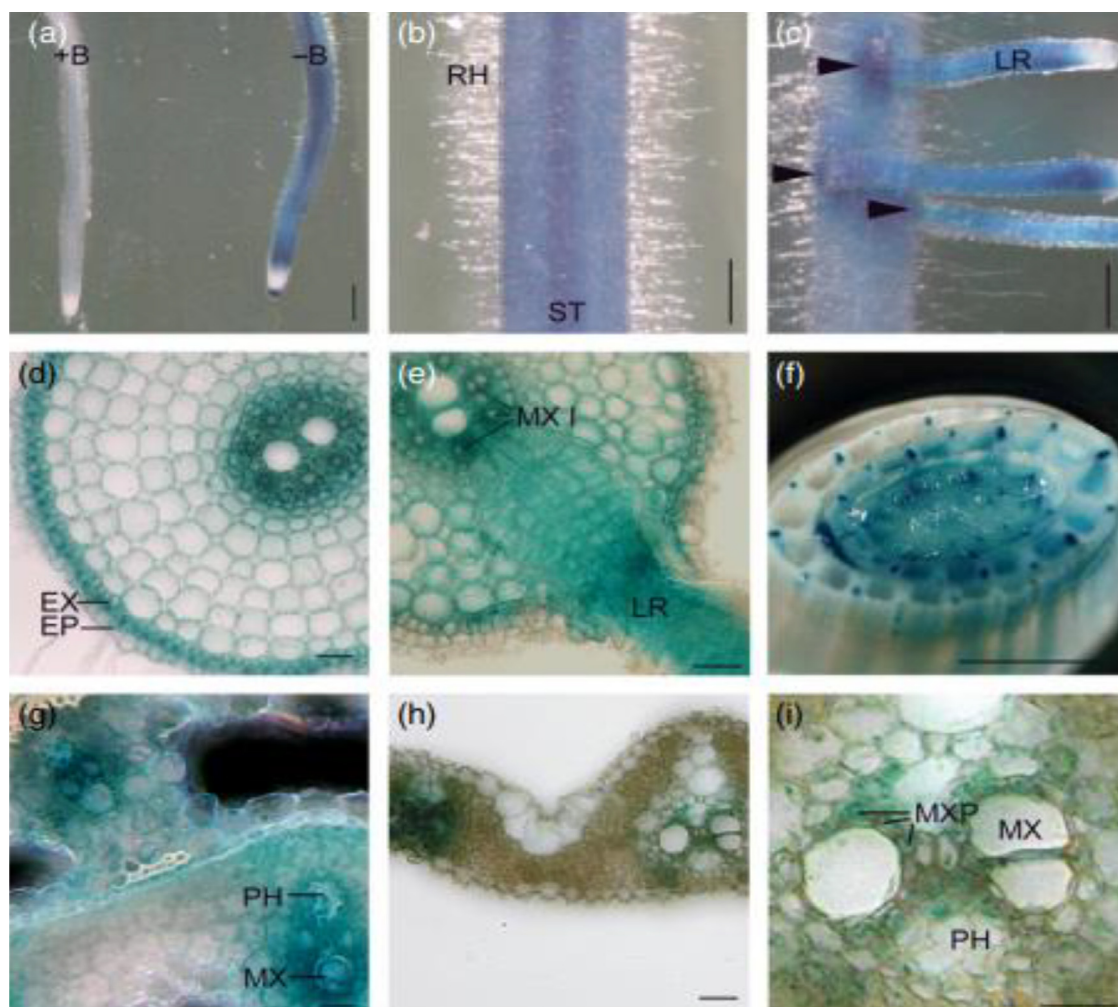


Fig. 1. GUS staining in *OsNIP3;1* promoter–GUS transgenic rice plants. (a) Primary roots of 14-days old rice plants grown in 18 μ M boron (+B) containing medium or devoid of boron (–B) medium. (b and c) Main roots of rice plants grown in –B condition as visualized using a stereoscopic microscope (d and e) Transverse section (T.S.) of a main root without and with lateral root of the same plants (grown under –B). (f) Leaf sheath of rice plants grown in –B condition imaged by stereoscopic microscope (g and h) T.S. of a leaf sheath and a leaf blade (grown under –B). (i) magnified view of a vascular bundle. Abbreviations- Epidermis (EP), Exodermis (EX), Lateral root (LR), Metaxylem (MX), Metaxylem parenchyma cell (MXP), Phloem (PH), Root hair (RH), Stele (ST). Scale bars = 1 mm (a–c, f) and 50 μ m (d, e, g–i) (Adopted with permission from Hanaoka et al., 2014).

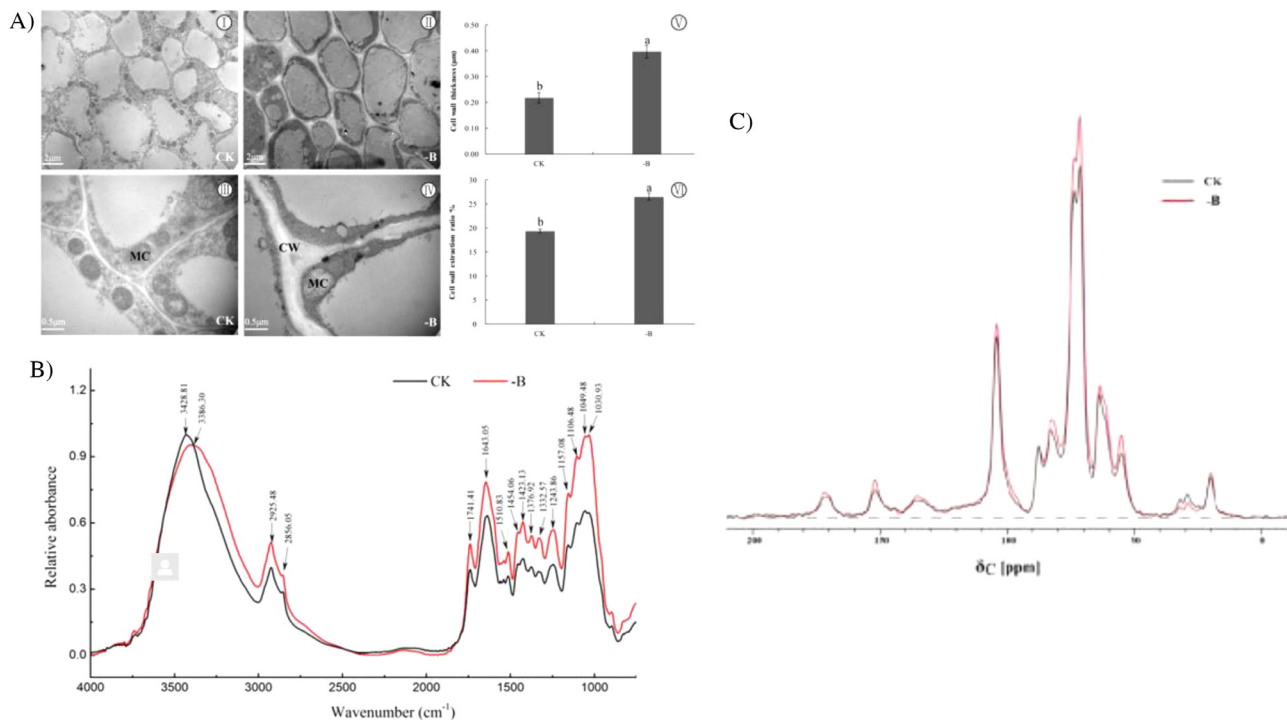


Fig. 2. Figure subpanel A) is showing the modifications in cell wall and subcellular structure under 10 μM boron (CK) and 0 μM boron (-B) treatments. I, II, III, IV represent root cell TEM micrographs; V and VI display thickness of cell wall (CW) and cell wall extraction ratio. Subpanel B)- FTIR spectral analysis of alterations in cell wall structure and composition under CK and -B conditions. Subpanel C)- ^{13}C NMR spectra in root cell walls under CK and -B conditions (Adopted from Wu et al., 2017; available at CC BY-4.0).

probably up as many as three times in euphyllophytes) (Jones and Dolan 2012; Niklas 2016; Kutschera and Niklas, 2017). Additionally, certain existing tracheophytes, such as *Psilotum nudum* (like some eusporangiate “ferns”) and some angiosperms, have lost or repressed their capacity to form roots (e.g., *Wolffia rrhizal*) (Kutschera and Niklas 2015). Roots’ evolutionary origins are regrettably ambiguous since it can be difficult to identify whether roots are absent as in certain extant pteridophytes, not preserved for a specific fossil, or possibly not discernible in a fossilized circumstance (Kutschera and Niklas 2017). The dearth of defined developmental features that can be utilized to identify “roots” precisely and accurately is another aspect of studying root evolution effectively (Kutschera and Niklas 2017). The deduction of growth of root has been contemplated in several plants like grapevine (Gunes et al., 2006), wheat (Turan et al., 2009), and tomato (Cervilla et al., 2009). Boron intoxication specifically led to aberrant cell division in the meristematic regions of broad bean roots (Liu et al., 2000), an establishment of the hypodermis, and enhanced deposition of suberin in the cortical cell walls of the soybean root (Ghanati et al., 2005). Nevertheless, lignification was not thought to be an important component for Boron-induced root development suppression in tomato plants (Cervilla et al., 2009). A high B concentration-induced localized suppressive response was observed in the root tip of wheat but not in the mature rhizosphere (Reid et al., 2004). Like, colchicine, excessive B induced cytotoxic effects during mitosis, on root tip cells, causing the production of stickiness in chromosomes, fragmented chromosomes, bridges formation and development of micronuclei (Liu et al., 2000; Konuk et al., 2007). A mathematical model predicted that the more proximal part of the meristematic zone has a lower B concentration; however, near the root tip has the maximum (Shimotohno et al., 2015). Additionally, the model indicated that B absorbed in the root tip was not effectively transported to shoots, indicating that B absorbed in the root tip was likely employed for local growth of root and that B transferring towards the shoot occurred in the more developed root regions (Shimotohno et al., 2015). In root of *Arabidopsis*, the molecular

mechanism of B toxicity-induced suppression of root development has been extensively studied (Aquea et al., 2012). The toxicity of B increased the gene expression related to cell wall modification, and abscisic acid responses/signalling. Excess B response in the root system has been hypothesized in terms of genotypic variations during root growth and elongation. These variations have been considered as indicators of B tolerance in plants (Hayes and Reid, 2004; Choi et al., 2006; Princi et al., 2016). A significant reduction in root development and the process of mitosis (cytogenotoxicity) have been observed due to B-toxicity (phenylboronic acid) through *Allium cepa* test (Khalil et al., 2017). B tolerance in barley corresponds to morphological changes in the roots that enhance branching and promote finer root development, thus enabling improved soil exploitation because of osmotic adjustment (Choi et al., 2007). Princi et al. (2013) studied that the significant impact of short-term B-excess therapy has been observed on several root morphological traits. To be more specific, in the presence of B excess, the tolerant tomato had a thinner and longer root system than the sensitive one. Further, Wu et al. (2017) clearly suggested the influence of B-insufficient condition impacts on the root tips of trifoliate orange roots. Over all the availability of boron significantly influenced the growth, development traits and transport of plants roots in normal as well as in challenging environment (Figs. 1 & 2)

1.2. Boron transport mechanisms and localization in roots: recent insights for transporters and channels

To circumvent B deficiency and toxicity issues, understanding of transporters and channels involve in the B uptake by root tissues is crucial (Takano et al., 2008). For living organisms, excess B is harmful. Boron binds to the cis-diol and inhibits the actions of substances containing cis-diol, including RNA, ATP, and NAD⁺ (Reid et al., 2004). These outcomes raise concerns about the transport of B through biological membranes. Without interacting with biomolecules, B, mostly found as boric acid in neutral solution ($\text{pK}_a = 9.24$) $[\text{B}(\text{OH})_3 + \text{H}_2\text{O} = \text{B}$

$(\text{OH})_4^- + \text{H}^+$], which is a weak Lewis acid. The monobasic boric acid can be passively diffused through biological membranes very easily since it is a small neutral molecule (Schnurbusch et al., 2010). Following the mass flow phenomenon, B is directed to the roots so that this nutrient may be absorbed from the soil solution (Marschner, 2012). The B uptake mechanisms are predominantly regulated by both metabolic and non-metabolic activities. However, some research data revealed a considerable variation in total B content and concentration between various species and genotypes cultivated under same circumstances (Nejad and Etesami, 2020). As a result, this shows that the variations in the membrane's permeability to boric acid may be the source of the discrepancies in B absorption between species (Huang and Graham, 1990; Hu and Brown, 1997) and the B absorption through lipid bilayers occurs through a combination of transport mediated channels and passive transport (diffusion) (Reid, 2014). B transporter activity is closely controlled as a reaction to B concentrations in the soil solution, maximizing absorption of B and utilization and preserving nutritional homeostasis in various tissues of plants (Takano et al., 2008; Yoshinari and Takano, 2017; Fig. 3). Mainly three mechanisms or pathways are recognized for the uptake and transport

of boron in plants: facilitated transport via channel proteins, such as Nodulin 26-like intrinsic proteins (NIPs); passive diffusion through plasma membrane; and high-affinity active transport by borate transporters (BOR) under low B availability (Brown et al., 2002; Takano et al., 2008; Miwa and Fujiwara, 2010).

Plants regulate B acquisition and its transport through two types of transporters, (i) the major intrinsic proteins (MIP) family, and (ii) the borate transporters (BORs) family (Matthes et al., 2020). The principal B transporters are the Nodulin 26-like intrinsic protein (NIP) sub-family (unique to plants), belongs to the MIP family, and have the ability to transport small and uncharged molecules. NIP5;1 was the first boric acid channel identified in *Arabidopsis thaliana* under limited B availability (Takano et al., 2006). In *Arabidopsis*, AtNIP6;1 is known to transport B to the growing plant parts under deficient B conditions, whereas AtNIP5;1 is the responsive channel for initial B uptake (Takano et al., 2006; Tanaka et al., 2008). Similarly, in rice, OsNIP3;1, a closest homolog at AtBOR1, regulates B distribution in shoot of plant and increase the growth of plant (Hanaoka et al., 2014). NIP5;1 favorably exists on the plasma membrane with its polarization towards the soil side (distal) (Takano et al., 2006; Wang

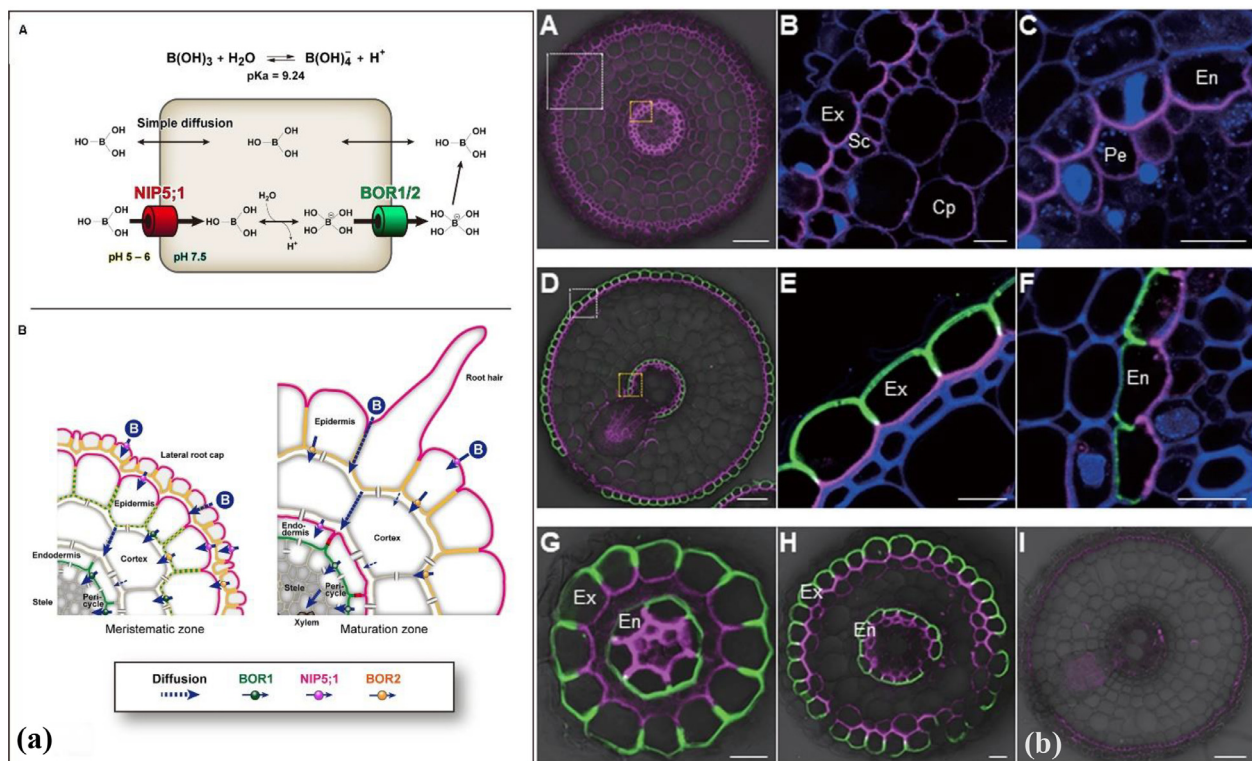


Fig. 3. Figure subpanel (a) shows the systematic models of transport pathways of boron (a) (A) In the apoplast, characterized by a low pH, borate anions are reconverted into boric acid, allowing BOR transporters to establish an uphill boric acid gradient. Boron transport and homeostasis rely on three primary mechanisms across the plasma membrane (PM). The first mechanism involves passive diffusion of uncharged boric acid across the lipid bilayers. The second mechanism is facilitated diffusion through boric acid channels, such as *Arabidopsis* NIP5;1, belonging to the NIP II family. The third mechanism involves export of borate via transporters like *Arabidopsis* BOR1 and BOR2. Under physiological conditions, boric acid channels enable the uptake of boric acid into cells. Once inside, the relatively high pH of the cytoplasm converts boric acid into borate anions, which are then exported through borate uniporters driven by the electrochemical gradient. In the apoplast, having a low pH, borate anions are rapidly re-converted to boric acid, allowing BOR transporters to build an uphill gradient of boric acid. (B) The expression of NIP5;1, BOR1, and BOR2 in *Arabidopsis* roots exhibits cell-type specificity under low-B conditions. NIP5;1 is expressed in the lateral root cap and epidermis of the meristematic zone and epidermis and endodermis of the maturation zone (Wang et al., 2017). BOR1 is localized and expressed in epidermis of the meristematic zone and in the endodermis of both meristematic and maturation zones (Yoshinari et al., 2016). BOR2 is expressed and localized in lateral root cap and epidermis in both these zones (Miwa et al., 2013). NIP5;1 is polarly localized to the soil-facing PM domain (Takano et al., 2010; Miwa et al., 2013). [Adopted from Yoshinari and Takano (2017), available at CC BY 4.0.] Subpanel (b): Polar localization of OsBOR1 and OsLsi1 in rice roots. Distribution of OsBOR1 and OsLsi1 in the root tip (A–C), mature region of crown roots (D–F), small (G), and large (H) lateral roots of transgenic line expressing functional *Flag-OsLsi1*. I shows the localization of OsBOR1 and *Flag-OsLsi1* in the crown root of *bor1-1* mutant. Enlarged views of the white or yellow-dotted areas in (A) and (D) are shown in (B, E) and (C, F), respectively. Root samples were collected from 25-days old seedlings grown in a solution without B for 3 days with sampling done from the root tip (3 mm from the root apex) and mature region (15 mm) of crown roots, and lateral roots. Double immunostaining was used to detect OsBOR1 and *Flag-OsLsi1*. Signals from OsBOR1 are shown in magenta, *Flag-OsLsi1* in green, and cell wall autofluorescence in blue. Root structures labels Ex stands for Exodermis, Sc for sclerenchyma, Cp for cortex parenchyma, En for endodermis, and Pe for pericycle. Scale bars = 10 mm except (A, D, and I), which are 50 mm. Adopted with permission from Huang et al., (2022a). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

et al., 2017); however, BOR1 located on proximal side, which play critical role in xylem loading of B (Wakuta et al., 2016; Yoshinari et al., 2019). Subsequently B get transported to the shoot along with the xylem flow (Matthes et al., 2020). Understanding the processes causing B transporters' variations in time and space is the fundamental challenge. A 2-D model (using a cross-sectional root meristem) of *A. thaliana* was created by coupling mathematics and experimental methods, considering the spatial subtleness, intensity of B transporters, and polarity (Shimotohno et al., 2015). Under low-B circumstances, AtBOR1 is essential for effective B translocation from the root-shoot systems (Takano et al., 2002; Jothi and Takano, 2023). AtBOR1 is situated in the plasma membrane, and it is polarised towards the stele side (Takano et al., 2010). However, in the trans-Golgi network/early endosome (TGN/EE), AtBOR1 is internalized and via multivesicular body/late endosomes (MVB/LEs) transported into the vacuole when plants are given larger amounts of boric acid (Takano et al., 2005; Takano et al., 2010; Viotti et al., 2010; Yoshinari et al., 2018). To prevent excessive B translocation to shoots, AtBOR1's vacuolar sorting should quickly deactivate the radial transport of B. Although AtBOR2, the most closely related paralog of AtBOR1, exhibits similar B-dependent polarization and vacuolar grouping, it serves a functional purpose distinctive from AtBOR1 (Miwa et al., 2013). The AtBOR2 mutants displayed decreased cell elongation of root in lesser-B supply circumstances. AtBOR4, in contrast, is thought to have a role in high-B tolerance. The overexpression of *AtBOR4* in *A. thaliana*, leads to high-B tolerance (Miwa et al., 2007) but shows high sensitivity to B-deficiency in roots (Miwa and Fujiwara, 2014). Under high B circumstances, AtBOR4 can therefore directly exclude B from the roots. These results suggest that the physiological role of BORs for low or high B tolerance is defined by the polarity and B-dependent degradation, which is an essential mechanism. To produce plants with increased nutrient usage efficiency, transporter modification is a promising strategy (Fig. 3). Kato et al. (2009) reported that improving root development in conditions of low B supply involves enhancing *NIP5;1* expression by introducing the 35S promoter (at 1357 bp upstream) of the *NIP5;1* gene. They further proved that higher tolerance for B deficiency can be conferred by the combination of increased *BOR1* and *NIP5* expression. *OsLsi1/OsNIP2;1* and *OsBOR1* mediate B absorption by the roots of rice (*Oryza sativa*). *OsLsi1* is a member of the NIP subfamily like *AtNIP5*; however, it is classified in a different subfamily (Ma et al., 2006; Mitani et al., 2008; Huang et al., 2022a, 2022b; Fig. 3b). *OsLsi1* was initially recognized as a silicic acid channel-type transporter (H_4SiO_4 ; Ma et al., 2006), permeable to H_3BO_3 (Mitani et al., 2008; Schnurbusch et al., 2010). It exists on the distal end of the endodermis and exodermis in rice roots (Ma et al., 2006; Pan et al., 2021; Gao and Chao 2022). Shao et al. (2018) investigated mutants in a physiological study in rice. They found that *OsLsi1* was an essential transporter for B absorption, as opposed to *OsNIP3;1*, a potential ortholog of *AtNIP5;1*. A substantial reduction in B uptake was recorded along with typical B-deficiency symptoms under lesser B conditions due to the knockout of *OsLsi1* (Shao et al., 2018). On other hand, as a B efflux transporter, *OsBOR1* is a close homolog of *AtBOR1* (Nakagawa et al., 2007; Shao et al., 2021; Huang et al., 2022a, 2022b). *OsLsi1* and *OsBOR1* develop a shared channel for the absorption of B in roots (Shao et al., 2021; Huang et al., 2022a, 2022b). There are homologs of *AtNIP5;1* and *AtBOR1* in *Zea mays* (Chatterjee et al., 2014; Durbak et al., 2014), *Brassica napus* (Zhang et al., 2017), *Triticum aestivum* (Pallotta et al., 2014), and *Hordeum vulgare* (Sutton et al., 2007; Schnurbusch et al., 2010) which have also been functionally characterized.

1.3. Boron and root architecture: relationship to phytohormones

In their natural habitat, plant evolved a complex network of hormonal signalling to modulate their development and adapt to a wide variety of abiotic and biotic stress. Different hormones play different

roles in growth and development of the plant, but they often have antagonistic or synergistic interactions in different developmental stages, different conditions of environment, or in different tissues. The serious plant hormonal signals are essential for controlling plants growth and development, continue to transmit signals to downstream pathways, and cope with the negative impacts of stress (Chen et al., 2023). Auxin is essential for cell differentiation and proliferation at the shoot and root meristems as well as for the subsequent growth of cells in the plants (Kohli et al., 2013). Boron deprivation affects the polar auxin transport from the root tip to the elongation zone and participates in the root growth process by promoting auxin redistribution (Martín-Rejano et al., 2011; Li et al., 2018; Fig. 4). Another crucial phytohormone that controls the growth of roots is called brassinosteroid (BR). A family of polyhydroxylated steroid phytohormones in plants is brassinosteroids (BRs). Cell elongation, reproductive development, root hair initiation, cell division, stomata formation, senescence, vascular differentiation, and photomorphogenesis are a broad range of physiological processes that BRs regulate (Divi and Krishna 2009; Wang et al., 2015; Wei and Li 2016). Several studies demonstrated the interaction of boron and BRs in plants such as Zhang et al. (2021) reveals that the micronutrient boron (B) is crucial for plant growth and development, and when plants are deficient in it, their root growth is immediately curtailed and the accumulation of brassinolide is reduce which ultimately downregulate BR signalling and modulate root elongation. Hormones function as endogenous regulatory factors that control this response by assisting plants in adjusting their growth to changes in nutrient availability (Rubio et al., 2009). Numerous studies demonstrate that cytokinin, either alone or in combination with another hormone, like ABA, auxin, or ethylene, play a special role in regulating and modulating plant responses to various nutritional stresses (Martin et al., 2000; Franco-Zorrilla et al., 2002; Takei et al., 2002; Sakakibara 2003; Franco-Zorrilla et al., 2004; Maruyama-Nakashita et al., 2004; Franco-Zorrilla et al., 2005; Nam et al., 2012; Li et al., 2021). Total root growth is influenced by two mechanisms: enlargement (in the elongation zone) and cell division (commonly in the meristematic region of the root). Numerous physiological studies on *Arabidopsis* plants demonstrate that B deficiency reduces the lengthening of primary root cells, a process that is regulated by interactions between ethylene and auxin, as well as among other possible intermediates (Martín-Rejano et al., 2011; Camacho-Cristóbal et al., 2015; González-Fontes et al., 2016). As a result, the primary root shows lower growth. The root development of *Arabidopsis* plants exposed to B deficiency has additionally been shown to be inhibited via cytokinin-mediated suppression of cell proliferation in the meristematic region of the root (Abreu et al., 2014; Poza-Viejo et al., 2018). It has been also reported that cytokinin play a crucial role in root development after interaction with other hormones such as it inhibits root development by interacting with auxin, and the auxin influx-carrier AUX1- and ethylene under boron deficiency (Dello et al., 2008; Hansen et al., 2009; Schaller et al., 2015; Streer et al., 2016; Herrera-Rodríguez et al., 2022). Further González-Fontes et al. (2016) has also described the interactive responses of boron deficiency and ethylene in root development. The ethylene-insensitive2 (EIN2) protein is participated in induction of root hair formation and elongation under Boron deficiency in *Arabidopsis thaliana* (Martín-Rejano et al., 2011). The impact of low B availability or B deficiency on root hair length was diminished in the presence of Ag^2+ , an inhibitor of the ethylene reaction (Camacho-Cristóbal et al., 2015). The findings of a detailed study by Tao et al. (2023) demonstrated that in *Arabidopsis*, B deficiency boosts auxin biosynthesis in shoots through improving the expression levels of auxin biosynthesis-related genes as well as encourages the polar auxin transport from shoots to roots by regulating their respective genes which ultimately in due courses resulting in auxin accumulation in root apices and root growth inhibition (Fig. 4). Overall, the above discussion suggests the important interactive responses of different

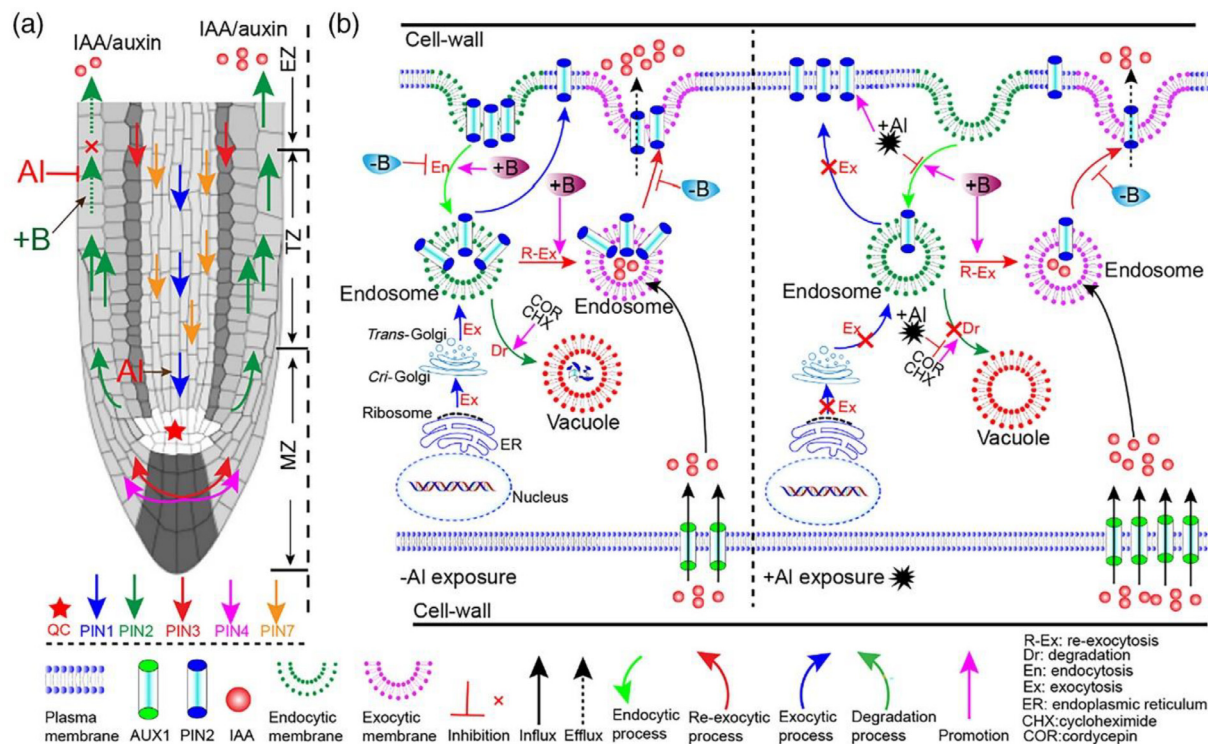


Fig. 4. Proposed model illustrating the transport pathways of auxin in Arabidopsis roots and their regulation by boron and aluminium. (a) Auxin transporters PIN1, 3, 4 and 7 located in stele and pericycle coordinate to control the transport of auxin from shoot to the quiescent centre (QC) of the root apex. Then PIN2 carriers (located at plasma membranes of epidermal cells) conducts the redistribution of auxin from QC to the root elongation zone. The PIN1 gene expression in root apex is up-regulated under Al stress while endocytosis of PIN2 membrane proteins is repressed by Al stress, resulting in enhanced accumulation of auxin in the root apical meristem (MZ) and transition zone (TZ) and decreased auxin transport to the root elongation zone (EZ). However, application of boron mitigates the Al-induced auxin transport inhibition from MZ to EZ. b) Proposed model of efflux of auxin from the epidermal cell of the root apical TZ. PIN2 endocytosis and its vesicle recycling is inhibited by boron deficiency, while boron application mitigates this effect. Endocytosed PIN2 proteins co-localize with IAA in endosomes, and the recycling of these endosomes (having both IAA and PIN2 proteins) facilitates efflux of auxin. Inhibitors such as CHX (proteins synthesis inhibitor) and COR (transcription inhibitor) induce PIN2 proteins degradation and are inhibited by Al stress. Al inhibits the PIN2 proteins endocytosis at the post-transcriptional level, while B supply not only promotes the PIN2 endocytosis but also increases its re-exocytosis, to counter-act the Al-induced auxin efflux inhibition the TZ. Adopted with permission from Tao et al. (2023).

phytohormones with boron availability for the root development in plants (Fig. 4).

1.4. Boron and signaling molecule interplay impact on root development

The life cycle of plants faces several biotic and abiotic stressors such as salinity, drought, heavy metals, and extreme temperatures during various growth stages of plants. As protection mechanisms, there are several stress-signaling phenomena through the release of plant signaling molecules which works significantly to repair the damage in plant system (Paul and Roychoudhury, 2020). Two major signaling molecules including nitric oxide and hydrogen sulphide have been found useful to regulate gene expressions, mediate cross-talk with other plant growth substances, and regulate post-translation modifications (PTMs) (Asgher et al., 2017; Spoel, 2018; Corpas et al., 2019; Prakash et al., 2019). Studies suggested a very interesting and useful interaction of boron along with different signaling molecules in plants suggests numerous modifications in cellular activities; however, there is still inadequate knowledge concerning the perceptiveness of plant symptoms of B along with the signalling molecules (González-Fontes and Fujiwara, 2020). Further, the concentration of cytosolic calcium $[Ca^{2+}]_{cyt}$ increases due to B-deficiency after 6–24 h in the roots of *Arabidopsis thaliana* (Quiles-Pando et al., 2019). However, Quiles-Pando et al. (2019) further suggested that some calcium ions influx across the plasma membrane from the apoplast even though some Ca^{2+} also comes from the vacuoles through the tonoplast channel (CNCC19). However, application of sufficient amount of Boron significantly restore the Ca^{2+} in plant cells for 24 h (Quiles-

Pando et al., 2019). Similarly in another study, the seedlings of *Arabidopsis thaliana* showed an increase in NADPH oxidase activities due to B-deficiency leading to an inhibited root elongation via an ethylene/auxin/ROS-dependent pathway (Camacho-Cristóbal et al., 2015). In addition, Wang et al. (2010) stated that, H_2S (Hydrogen sulfide) is emerging as a potential messenger molecule involve in modulation of physiological processes in plants. In the study he found that, treatment with H_2S donor mitigated the B toxicity induced inhibition of elongation of root in cucumber (*Cucumis sativus*) seedlings.

The role of gibberellic acid (GA) induced rise in production of Hydrogen sulfide (H_2S) in alleviating tolerance to boron toxicity (BT) in tomato plants has been well identified (Kaya et al., 2020a, 2020b). GA mitigated BT by enhancing the endogenous H_2S i.e. sodium hydrosulfide and leaf Ca^{2+} and K^+ , and decline the contents of leaf H_2O_2 , MDA, and B as well as membrane leakage (Kaya et al., 2020a, 2020b). In another study by Kaya and Ashraf (2015), reveals that exogenous NO can overcome the deleterious effects of B toxicity on tomato fruit yield and whole plant biomass by reducing the concentration of Boron, MDA and H_2O_2 as well as electrolyte leakage. In addition, Kaya et al. (2020a, 2020b) further suggested the role of thiamine induced significant improvement of endogenous synthesis of nitric oxide which may function as a downstream signal in THI-induced tolerance to B toxicity in pepper (*Capsicum annuum* L.) plant. Similarly, SNP (NO donor) has been found to manage the boron induced toxicity in maize (*Zea mays* L.) seedlings through regulation of oxidative damage, electrolyte leakage and growth traits (Esim and Atici, 2013). Further Zhu et al. (2019) demonstrated the B induced alleviation of Al toxicity in rice in which Boron significantly decreases

the decomposition of Al in the cell wall of rice roots by inhibiting pectin synthesis and suppressing PME activity, which are related to changes in H_2O_2 contents in rice root. Taking into the account of above discussion on signalling molecules interaction with boron suggests a very prominent and interesting future research possibilities which may contribute and resolve several unfolded questions of this field however an extensive research including molecular studies are required.

1.5. Role of boron in root formation and secondary metabolites regulation under abiotic stress tolerance

Abiotic stress is recognized as one of the major threats to global crop production which not only affects the quantity of food production but also reduces the quality of different staple food crops. Most of the abiotic pressures on crops are becoming more prevalent because of climate change (Sánchez-Bermúdez et al., 2022). Although it has been stated that plants activate their self defence system including physiological, cellular, and molecular adapt and respond against several types of abiotic stresses (Srivastava et al., 2016). Similarly, Zhang et al. (2023a) suggested that plants have naturally evolved a variety of defense and tolerance mechanisms in reply to these stress signals that interact with one another. However, to overcome and to reduce the problem of abiotic stress, exogenous application of different nutrients, phytohormones, signalling molecules have been found very effective (Swain et al., 2023). Among the all allivators there is adequate manifest that boron can repair the damage of crops growing in adverse circumstances (García-Sánchez et al., 2020). It is widely recognized that Boron plays an essential role in the metabolism and transport of carbohydrates, while under salt stress, carbohydrate changes are extremely important due to their correlation with processes like respiration and photosynthesis (O'Neill et al., 2004; Banerjee et al., 2021). Furthermore, the use of Boron reduces the deleterious effects of salt by maintaining cell wall flexibility and restoring K^+ levels because it participates in cell wall synthesis and construction as well as membrane structure and function (Shahid et al., 2018). It is further established that boron supplementation drastically recovers the nutrient imbalance and thus salinity stress in nitrogen-fixing legume plants (Venugopalan et al., 2021). Marschner 2012 It has been discovered that B nutrition enhances photosynthetic efficiency, sugar transport, lipid metabolism, hormone synthesis, seed and grain production, flower retention, pollen generation, and seed germination in plants, enhancing their resilience to drought stress (Rufat and Arbonés, 2006; Wróbel, 2009; Marschner 2012; Da Silva et al., 2015; García-Sánchez et al., 2020). A further benefit of Boron-nutrient-rich plants' enhanced tolerance to drought stress as they produce more root hairs and mycorrhizae, which increases water absorption from the rhizosphere of the soil (Rufat and Arbonés 2006; Wróbel 2009; Da Silva et al., 2015). Aluminium toxicity limits the plants growth by inducing inhibition of root elongation. Riaz et al. (2018b) revealed that aluminium toxicity led to higher accumulation of aluminium to cell wall that result in altered cell wall structure in plants. Nevertheless, application of boron (10 μ M and 50 μ M) in trifoliate orange roots increased root elongation by decreasing Al^{3+} accumulation to cell wall and reducing the distribution of HG epitopes in the plant roots (Riaz et al., 2018a). Riaz et al. (2021) further suggested that Cd stress has detrimental effect on the growth traits, so by applying boron (0 and 30 μ M) reduced Cd uptake and concentration in plant tissue and enhancing antioxidant defense system in roots of rice (*Oryza sativa*) seedlings. Moreover, Chen et al. (2022) demonstrated that Boron-supplementation lowered Cu-toxicity involved reduced damage to roots growth and function and improve nutrients and water status in sweet orange (*Citrus sinensis* L.) seedlings. In hot pepper (*Capsicum annuum*), with the application of B upregulated sulphur metabolism-related genes in the root and reduces the translocation, uptake, and accumulation by retaining Cd

stress in the roots cell walls and reducing GSH content (Huang et al., 2022b). Another study reported by Shireen et al. (2021) concluded that vanadium stress severely reduced root and shoot growth and increased the accumulation of ROS. In watermelon, mechanism of Boron (75 μ M) induced vanadium stress tolerance in the cell wall and promoting boron transport, increased antioxidant defense system which ultimately improved the growth of watermelon (Shireen et al. (2021). Metabolic networks in plants need to be modified under unfavourable environments to retain the required metabolism (Obata and Fernie, 2012). Plants adopt an essential defense procedure in response to dealing with various abiotic stressors, including dissimilarity in their metabolic and metabolite pathways (Zhang et al., 2023b). The roles of boron in several plant metabolites have undergone extensive research and its deprivation can affect a change in a broad variety of metabolites, including phenolic compounds, carbohydrates, and amino acids (Bolaños et al., 2004; Dordas and Brown, 2005; Beato et al., 2010). The functions of B in these metabolites are still main contested, and the extensive studies have still not done to explore the Boron functions in various metabolic pathways. Currently, metabolomics analysis has mostly been employed to investigate the alterations brought on by abiotic stress in a variety of unique metabolites (Armengaud and Gibon, 2009; Takahashi et al., 2012; Foito et al., 2013; Sung et al., 2015). Alves et al. (2011) examined that metabolomics technology was used to examine how B deficiency affected the metabolites in various organs of *Lupinus albus* plant and showed that it changed the amino acid profiles. Beato et al. (2011) stated that, according to metabolomic analysis, tobacco roots' levels of different phenolics, organic acids, and amino acids enhanced after 24 h of B deficiency. Overall, the studies discussed above clearly demonstrated the suitability and significant impacts of boron against the abiotic stress in plants which open the possibility to explore its more beneficial uses through novel biotechnological techniques including genome editing to prepare the new varieties of crops resistance against the abiotic stresses.

1.6. Conclusion and future prospective

For the growth and development of higher plants, boron is an essential microelement, it is hazardous to sensitive plants when present in excess amounts. B usually accumulates to hazardous levels for crops in saline/alkaline soils that are associated with inadequate rainfall, over fertilised, and/or irrigated with B-rich water. Thus, soil containing B toxic levels is a global issue for agricultural quality and productivity, particularly in semiarid and arid regions. The range between scarce and dangerous B levels is less compared to any other nutritional element, and Boron requirements are highly variable between plant species. The interaction of boron with other stresses is very complex, as various factors come into play such as B chemistry in plants, transpiration, damage caused in the plants by other stresses. Based on numerous studies, we can conclude that boron is involved in phytohormones signalling, root formation during abiotic stress, and also in secondary metabolites for the development of plant. Taking together the importance and essentiality of boron in plant life and its involvement in metabolic processes, it is important to explore some more deeper and detailed insights of boron research in plant system. This can open several ways to not only manage the boron deficiency and toxicity issues in plant system but also scientist can prepare the new resistant plant varieties of staple food crops through modern biotechnological tool and techniques which can survive in adverse condition and can contribute to resolve the global food hunger through feed global population.

Declaration of competing interest

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

CRediT authorship contribution statement

Aakriti Srivastava: Writing – original draft. **Monika Thakur:** Writing – review & editing. **Sangeeta Pandey:** Writing – review & editing. **Chitrnanjan Kumar:** Writing – review & editing. **Shivesh Sharma:** Writing – review & editing. **Rupesh Deshmukh:** Writing – review & editing. **Anket Sharma:** Writing – review & editing. **Vijay Pratap Singh:** Writing – review & editing. **Durgesh Kumar Tripathi:** Conceptualization, Formal analysis, Resources, Supervision, Writing – review & editing.

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