



Boron nutrition of rice in different production systems. A review

Atique Ur Rehman, Muhammad Farooq, Abdul Rashid, Faisal Nadeem,
Sabine Stuerz, Folkard Asch, Richard W. Bell, Kadambot H.M. Siddique

► To cite this version:

Atique Ur Rehman, Muhammad Farooq, Abdul Rashid, Faisal Nadeem, Sabine Stuerz, et al.. Boron nutrition of rice in different production systems. A review. *Agronomy for Sustainable Development*, 2018, 38 (3), pp.25. 10.1007/s13593-018-0504-8 . hal-02973741

HAL Id: hal-02973741

<https://hal.science/hal-02973741>

Submitted on 21 Oct 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Boron nutrition of rice in different production systems. A review

Atique-ur-Rehman^{1,2} · Muhammad Farooq^{1,3,4,5} · Abdul Rashid⁶ · Faisal Nadeem¹ · Sabine Stuerz⁴ · Folkard Asch⁴ · Richard W. Bell⁷ · Kadambot H. M. Siddique⁵

Accepted: 15 April 2018 / Published online: 1 May 2018
© INRA and Springer-Verlag France SAS, part of Springer Nature 2018

Abstract

Half of the world's population—more than 3.5 billion people—depend on rice for more than 20% of their daily energy requirements. Rice productivity is under threat for several reasons, particularly the deficiency of micronutrients, such as boron (B). Most rice-based cropping systems, including rice–wheat, are facing B deficiency as they are often practiced on high pH and alkaline soils with low B contents, low soil organic matter, and inadequate use of B fertilizer, which restricts the availability, uptake, and deposition of B into grains. Farmers' reluctance to fertilize rice fields with B—due to the lack of cost-effective B-enriched macronutrient fertilizers—further exacerbates B deficiency in rice-based cropping systems. Here we review that, (i) while rice can tolerate excess B, its deficiency induces nutritional disorders, limits rice productivity, impairs grain quality, and affects the long-term sustainability of rice production systems. (ii) As B dynamics in the soil varies between flooded and aerobic rice systems, different B deficiency management strategies are needed in rice-based cropping systems. (iii) Correct diagnosis of B deficiency/toxicity in rice; understanding its interaction with other nutrients including nitrogen, phosphorus, potassium, and calcium; and the availability and application of B fertilizers using effective methods will help to improve the sustainability and productivity of different rice production systems. (iv) Research on rice-based systems should focus on breeding approaches, including marker-assisted selection and wide hybridization (incorporation of desirable genes), and biotechnological strategies, such as next-generation DNA and RNA sequencing, and genetic transformations to develop rice genotypes with improved B contents and abilities to acquire B from the soil. (v) Different B application strategies—seed priming and foliar and/or soil application—should be included to improve the performance of rice, particularly when grown under aerobic conditions.

Keywords Boron · Breeding · Molecular biology · Plant physiology · Rice-based production systems

✉ Muhammad Farooq
farooqcp@gmail.com

- ¹ Department of Agronomy, University of Agriculture, Faisalabad 38040, Pakistan
- ² Department of Agronomy, Bahauddin Zakariya University, Multan, Pakistan
- ³ Department of Crop Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, 123 Al-Khoud, Oman
- ⁴ Institute of Agricultural Sciences in the Tropics, University of Hohenheim, 70599 Stuttgart, Germany
- ⁵ The UWA Institute of Agriculture and School of Agriculture and Environment, The University of Western Australia, LB 5005, Perth, WA 6001, Australia
- ⁶ Pakistan Academy of Sciences, Islamabad, Pakistan
- ⁷ School of Veterinary and Life Sciences, Murdoch University, Murdoch, WA 6150, Australia

Contents

- 1 [Introduction](#)
- 2 [Boron in plant biology](#)
 - 2.1 [Cell wall strengthening](#)
 - 2.2 [Membrane function](#)
 - 2.3 [Photosynthesis](#)
 - 2.4 [Assimilate partitioning](#)
 - 2.5 [Reproductive growth](#)
 - 2.6 [Boron concentrations and requirements in plant parts](#)
- 3 [Boron in soil and its dynamics in rice production systems](#)
 - 3.1 [Flooded rice system](#)
 - 3.2 [Aerobic rice system](#)
- 4 [Factors affecting boron availability to rice](#)
 - 4.1 [Soil characteristics](#)
 - 4.1.1 [Soil pH](#)
 - 4.1.2 [Soil salinity](#)
 - 4.1.3 [Soil organic matter](#)
 - 4.1.4 [Soil adsorption](#)

- 4.2 [Interaction with other nutrients](#)
 - 4.2.1 [Nitrogen](#)
 - 4.2.2 [Phosphorus](#)
 - 4.2.3 [Potassium](#)
 - 4.2.4 [Calcium](#)
- 4.3 [Environmental factors](#)
 - 4.3.1 [Light intensity](#)
 - 4.3.2 [Relative humidity](#)
- 4.4 [Boron interaction with soil biota](#)
- 5 [Diagnosing boron deficiency in rice](#)
- 6 [Managing boron deficiency in rice](#)
 - 6.1 [Yield and grain quality enhancement with boron fertilization](#)
 - 6.2 [Boron fertilization](#)
 - 6.2.1 [Sources of boron](#)
 - 6.2.2 [Boron application methods](#)
 - 6.2.2.1 [Soil application](#)
 - 6.2.2.2 [Foliar application](#)
 - 6.2.2.3 [Priming/coating strategies](#)
 - 6.2.3 [Residual effect of soil-applied boron fertilizer](#)
 - 6.3 [Boron cycling in rice-based agroecosystems](#)
 - 6.4 [Boron use recommendations](#)
 - 6.5 [Boron toxicity hazard in rice?](#)
 - 6.6 [Constraints to fertilizer boron user](#)
- 7 [Improving boron utilization and partitioning](#)
 - 7.1 [Conventional breeding](#)
 - 7.2 [Molecular and biotechnological approaches](#)
 - 7.3 [Agronomic approaches](#)
- 8 [Conclusions and future research thrusts](#)
- [Funding Information](#)
- [References](#)

1 Introduction

Food security is under threat due to stagnant yields of the main staple food crops (FAO 2016). Rice (*Oryza sativa* L.) is an important grain with about 50% of the world's population depending on it as their staple food, particularly in fast-growing and population-dense regions of the world (Fageria and Baligar 2003). Rice provides 21% of the energy and 15% of the protein requirements of human populations globally (Maclean et al. 2002; Depar et al. 2011). The prevalent rice production systems are lowland (puddled-transplanted) and upland rice (grown under rainfed conditions without standing water) (GRiSP (Global Rice Science Partnership) 2013). While some rice is grown in various developed countries, it is more significant in low-income and low-middle-income countries, where it accounts for 19% of the total cropped area (GRiSP 2013). To save water, rice is increasingly cultivated without standing water (Stuerz et al. 2014). While increased wages, labor scarcity, water shortages, and nutrient mining are concerns for successful rice production, micronutrient

deficiencies (particularly boron) are an emerging threat (Pandey and Velasco 1999; Sharma and Nayyar 2004; Tuong et al. 2005; Rashid et al. 2004, 2007).

Boron (B), a nonmetal micronutrient, is essential for normal growth and development of plants, including rice (Gupta 1979; Dunn et al. 2005); its essentiality was first reported in 1933 (Warington 1933). Boron deficiency affects the yield of 132 crops in at least 80 countries (Shorrocks 1997). Insufficient levels of available B in soils reduce crop yield, impair grain quality, and increase the susceptibility of crops to diseases (Fig. 1; Goldbach et al. 2007). However, B requirements vary among plant species (Bell 1997) and depend on factors such as soil type (calcareousness/alkalinity), soil moisture, pH, B concentration, soil organic matter, and plant species (Welch et al. 1991). Boron deficiency has been reported in rice-growing soils, where it causes substantial yield losses (Cakmak and Römheld 1997; Rashid et al. 2004, 2007). About 35% of the 2.6 million ha rice area in Pakistan (i.e., 0.91 million ha) suffers from B deficiency; both fine-grain Basmati and IRRI-type coarse-grain cultivars are adversely affected by boron deficiency (Rashid et al. 2017).

Boron is vital for essential plant functions as it is an integral component of rhamnogalacturonan II (RG-II) which acts as a binding fraction in cell walls and, therefore, supports membrane integrity, cell wall synthesis, and the indole acetic acid



Fig. 1 Boron nutrition in rice. **a** Adequate boron. **b, c** Boron deficiency (interveinal chlorosis and necrotic spots). **d** Boron toxicity

mechanism (Goldbach et al. 2001). Boron has been associated with one or more of the following processes: calcium utilization, cell division, flowering/reproductive phase, water relations, disease resistance, and nitrogen (N) metabolism (Sprague 1951; Goldbach et al. 2007; Ahmad et al. 2009). Boron deficiency in rice induces panicle sterility due to poor pollen and anther development and failed pollen germination and alters cell wall pectin in pollen tubes (Yang et al. 1999) which reduces the number of grains per panicle and, therefore, grain yield (Nieuwenhuis et al. 2000; Gowri 2005). Moreover, B deficiency in rice not only reduces paddy yield but also damages grain quality (Rashid et al. 2004, 2007). Conversely, B toxicity has also been observed in rice (Ponnamperuma and Yuan 1966) with symptoms including interveinal chlorosis in older leaves and dark brown elliptical spots on affected plant parts.

There is substantial literature available on the importance of B for agricultural productivity, B deficiency in soils and crops, and B involvement in plant structure and physiological function (Cakmak and Römhelt 1997; Blevins and Lukaszewski 1998; Ahmad et al. 2009, 2012), but little information on B nutrition in rice-based cropping systems. This review focuses on (1) the importance of B nutrition in rice-based cropping systems, (2) B function in plant physiology and its soil dynamics, (3) B interactions with other nutrients, (4) B deficiency and toxicity, (5) application methods, (6) management options, and (7) breeding and molecular tools to improve B nutrition in rice.

2 Boron in plant biology

Boron is an essential micronutrient with diverse roles in the physiological processes of plants. The primary function of B is undoubtedly its structural role in cell walls and the maintenance of plasma membrane functions (Brown et al. 2002; Wimmer et al. 2009). The reproductive stage of plants is far more sensitive to B deficiency than the vegetative phase (Ahmad et al. 2009). The B-specific transporter, BOR1, is actively involved in the regulation of B transport and its messenger RNA has been found in plant roots and shoots (Fig. 2; Takano et al. 2005). Moreover, B is necessary for the growth of meristematic tissues, pollen germination, cell division, membrane function, and assimilate partitioning.

2.1 Cell wall strengthening

Boron starvation alters the composition of cell wall components. For instance, B deficiency affects cellulose, hemicellulose, pectin, and lignin contents in cell walls. Cellulose, hemicellulose, and uronic acid concentrations increase while water-soluble pectin decreases (Zehirov and Georgiev 2003). Pectin and polysaccharide complexes,

along with homogalacturonans and rhamnogalacturonans I and II (RG-I and RG-II) are vital components of the cell wall (Reuhs et al. 2004). Boron and the RG-II complex are responsible for connecting sites for pectic polysaccharides through B-diester bonds (Matoh 1997), and borate-diester bonding helps in cell wall stabilization. Borate forms a cross-link with apiose residues of RG-II and contributes to a three-dimensional pectic network (O'Neill et al. 2004). Complexes formed due to B differ by steric organization of molecules; moreover, the pectic polysaccharide layer—comprising two branched-chain sugars that were found as residues in galacturonan-type pectin [apiose] on A and B side chains—stabilizes borate bridge forms by chain A. However, B chain did not contribute to RG-II dimer formation (Reuhs et al. 2004).

RG-II is considered the basic infrastructure for cell wall stabilization because of its highly complex structure and appearance of its genes during initial cell wall growth stages (Matsunaga et al. 2004). The RG-II B-complex is crucial for primary and secondary cell wall expansion and structure; the interaction of B with RG-II also occurs beyond cell wall cross-linking (Ryden et al. 2003; Kohorn et al. 2006). Small structural alterations in the RG-II complex can affect its stability; therefore, a higher ratio of B to RG-II is required for complex formation (Goldbach and Wimmer 2007). The RG-II group provides the connecting regions for pectin polysaccharide chains through B-diester bonding; however, if B deficiency occurs at binding regions, the ability of cell walls to retain pectin declines (Kobayashi et al. 1997). Under B deficiency, the pore size in cell walls increases, causing cell death when entering the elongation phase (Fleischer et al. 1999). Boron is vital for cell-to-cell adhesion and building cell wall infrastructure to maintain cell wall integrity (Bassil et al. 2004). Boric acid and borate interact with the diol group in the *cis* position, and borate forms esters with monosaccharides as well as the β -derythofuranose configuration (Tanaka and Fujiwara 2008).

2.2 Membrane function

Boron is vital for the function of enzymes and other proteins in the plasma membrane as well as its integrity and regulation of transport across the membrane (Cakmak and Römhelt 1997; Goldbach et al. 2001; Goldbach and Wimmer 2007). Boron deficiency induces the transformation of the membrane potential (Blaser-Grill et al. 1989) by increases in proton-pumping ATPase activity to develop a proton gradient across the plasma membrane (Obermeyer et al. 1996) and by inhibiting the activity of plasma membrane-bound oxidoreductase (Wimmer et al. 2009). Boron is necessary for the stabilization and integrity of membrane functioning through glycolipid binding (Brown et al. 2002). Boron deficiency rapidly alters ion fluxes due to the accumulation of

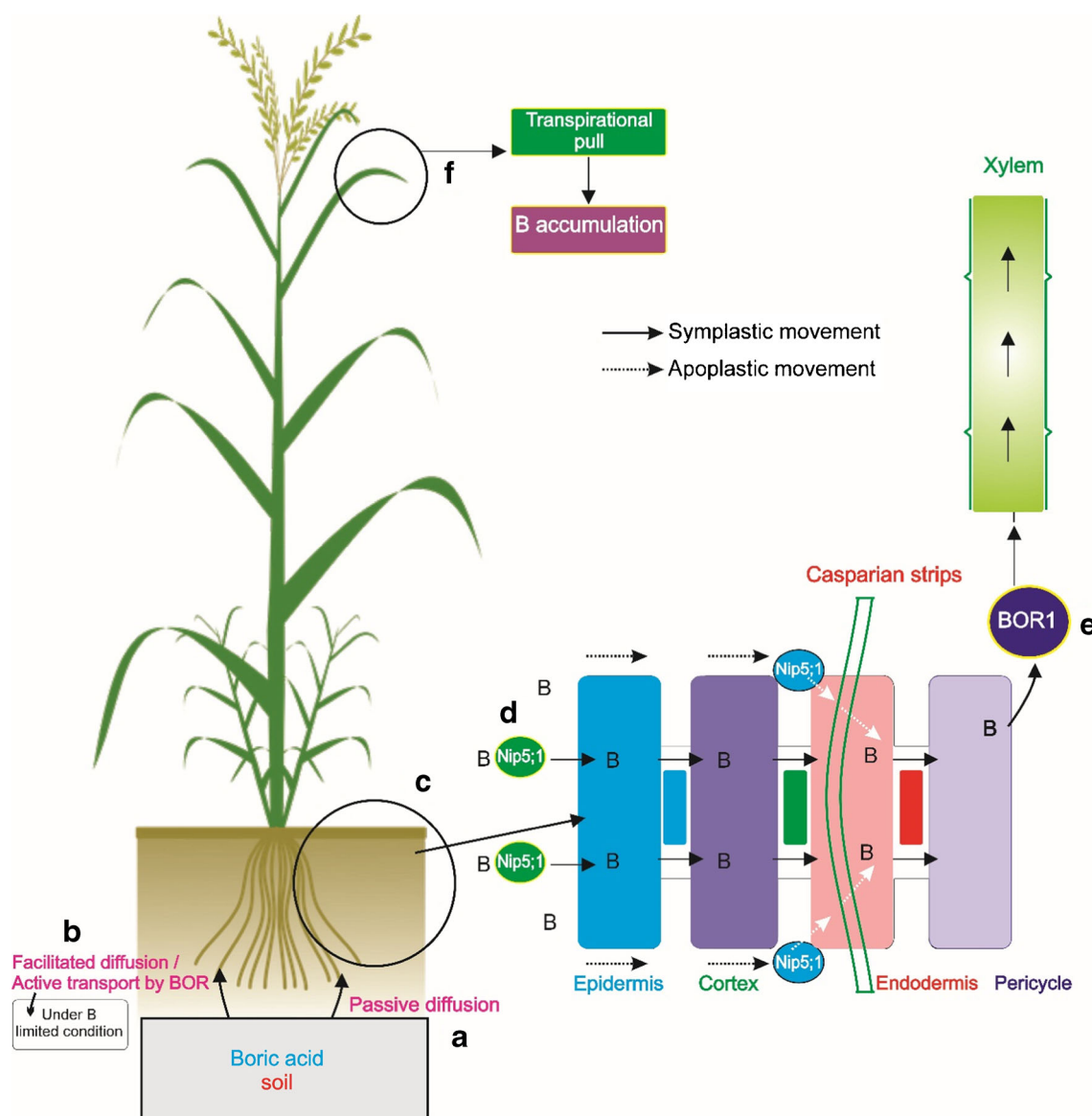


Fig. 2 Mechanism of boron (B) movement from soil to plant. (a) B is taken up by plant from the soil as ‘boric acid,’ an uncharged molecule. Under conditions of optimum availability, B is taken up by plants via passive diffusion. (b) Under B-deficient conditions, B movement occurs through active transport by BOR (a transporter) or facilitated diffusion mediated by channels such as NIP5;1. (c) Under low B conditions, NIP5;1 is expressed at the root epidermis and functions as B uptake channel. (d) NIP5;1 mediated the movement of B into the epidermis

and enters into the endodermis via the cortex. Casparian strip developed in the endodermis and endodermal cell is suberized and blocks the uptake of solute directly from the root apoplast. B enters into the pericycle via apoplastic pathways; symplastic movement facilitated by NIP5;1. (e) B is loaded into xylem via BOR1 (xylem loading efflux transporter). (f) Accumulation of B as function of transpiration pull. Symplastic movement represents transport from cell to cell. Apoplastic pathway refers to movement through extracellular spaces

phenolics and modulation of auxin-mediated activity of plasma membrane-bound H^+ -ATPases (Cakmak and Römhelt 1997). Boron deficiency results in membrane leakage due to a loss of membrane functional integrity (Cakmak and Römhelt 1997). Adequate supply of B may stimulate plasma membrane H^+ -pumping activity by increasing the driving force for K^+ influx (Cakmak and Römhelt 1997); obstruction of plasma membrane-bound [oxidoreductase] activities indicates direct interaction between B and membranes (Goldbach and Wimmer 2007).

2.3 Photosynthesis

Photosynthesis is not particularly sensitive to B deficiency or toxicity. However, its deficiency may indirectly affect photosynthesis by decreasing the photosynthetic area and altering leaf constituents (Dell and Huang 1997; Wang et al. 2007). Boron deficiency reduces chlorophyll and soluble protein contents in the leaves, and the resultant loss in photosynthetic enzyme activity obstructs the Hill reaction and decreases net photosynthesis (Sharma and Ramchandra 1990; Cakmak and

Römheld 1997; Brown et al. 2002). Although the exact mechanism is unknown, there is evidence that B deficiency disturbs the electron transport chain (ETC) in the thylakoid membrane, causing photoinhibition (Goldbach et al. 2007). Boron deficiency in the leaves substantially reduces photosynthetic oxygen evolution (42%), quantum yield, and the efficiency of the photosystem (PSII) ETC (Kastori et al. 1995; El-Shintinawy 2000) resulting in diminished photosynthesis (Wang et al. 2007). By damaging the plant phloem transport, reducing sink capacity, and increasing sugar accumulation in the leaves, B deficiency can cause downregulation of photosynthesis (Wimmer and Eichert 2013). Boron deficiency reduces the ability of the plant to capture light, which decreases photosynthetic activity (Cakmak and Römheld 1997). Poor leaf expansion under B-deficient conditions indirectly hampers photosynthesis (Furlani et al. 2003), because leaves deficient in B have low stomatal frequencies and smaller stomatal apertures, which both reduce stomatal conductance to CO₂ (Sharma and Ramchandra 1990). Moreover, B deficiency disrupts chloroplast structure and the functioning of chloroplast thylakoids that restrict CO₂ assimilation and lead to substantial reductions in photosynthesis (Pandey and Pandey 2008). Boron deficiency reduces the growth of root and shoot tips and the source/sink capacity of plants due to an oversaturation of electron acceptors of PSII or PSI (Goldbach et al. 2007). Boron deficiency may induce greater sensitivity of the photosynthetic machinery to abiotic stresses (Ye 2005). For instance, B deficiency enhanced chilling-induced photoinhibition in several tropical and subtropical plants (Huang et al. 2005).

2.4 Assimilate partitioning

Sugar transport is facilitated by B as it is an integral component of the sugar–borate complex, where boronic acid facilitates the efflux glucose and ribonucleosides from liposomes via artificial lipid bilayer membranes (Westmark et al. 1996; Dordas and Brown 2000). Under B-deficient conditions, the translocation of assimilates from source to sink declines, due to diminished sink capacity, which alters assimilate distribution in roots and shoots (Dugger 1983; Marschner 1995). In B-deficient source leaves, sugars and starch accumulate due to the reduction in assimilate translocation from the leaves to other organs (Kastori et al. 1995). The most prominent effects of B deficiency are reduced stem and fruit fractions and increased leaf fraction, which are attributed to the reduction in assimilate translocation to growing regions (Dixit et al. 2002). The rate of translocation and redistribution of assimilates to new growing points, particularly fruits, improved with adequate B nutrition (Hellal et al. 2009). In contrast, sucrose transport from mature to younger leaves decreased under B deficiency (Marschner 1995). At grain filling, adequate B nutrition is needed for optimum assimilate partitioning to

developing grains (Hussain et al. 2012). OsBOR1 in rice acts as an efflux B transporter, which is involved in B uptake and xylem loading (Nakagawa et al. 2007). A BOR1 homolog, YNL275w, also found in *Saccharomyces cerevisiae*, plays a role in B transportation across the plasma membrane (Takano et al. 2002). Boron transporters have been identified in flowers, pollen and, possibly, the upper stem and may play a role in B distribution and partitioning (Yoshinari and Takano 2017). Shelp (1988) reported enhanced N concentration and fluid accumulation in plant tissues under B-deficient conditions. Moreover, B deficiency affects nitrogen partitioning including relative amino acid [glutamine, alanine, asparagine] composition (Shelp 1990).

2.5 Reproductive growth

Historically, plant reproductive growth was considered more sensitive to B deficiency than vegetative growth (Dell and Huang 1997; Uruguchi and Fujiwara 2011; Rerkasem and Jamjod 2004). That is B deficiency in field crops is considered to reduce grain set more than vegetative growth. However, this was not the case for some field crops grown in B-deficient calcareous soils, such as wheat (Rashid et al. 2002a, 2011), rice (Rashid et al. 2002a, 2007), and rapeseed (Rashid et al. 2002b). In fact, in rice, B deficiency reduced straw biomass production more than paddy yield (Rashid et al. 2002a, 2007).

Under B deficiency, pollen grains appear empty, shriveled and misshapen, or normal but lacking starch reserves (Dell and Huang 1997). Pollen germination and pollen tube growth are impaired under B-deficient conditions as observed in rice (Wang et al. 2003; Lordkaew et al. 2013). In rice, B deficiency reduces panicle number and induces poor grain fertility (Rashid et al. 2007; Uruguchi and Fujiwara 2011). Huang et al. (2000) indicated a short critical period of microsporogenesis during which B deficiency retards anther development and lowers pollen viability of wheat. Low B reduces male fertility primarily by impairing microsporogenesis (Furlani et al. 2003). Boron in pollen cell walls is expected in the form of borate–RG-II complex, which provides a binding site for B in plants cell wall (Matoh et al. 1996, 1998). In rice, OsBOR4 is a B transporter with a crucial role in reproductive processes, such as pollen germination; under B deficiency, the activity of this gene is restricted (Tanaka et al. 2013). Lordkaew et al. (2013) reported B concentrations > 20 mg kg⁻¹ for rice pollen viability and grain set. Boron deficiency at the reproductive stage caused abnormal stomata and distorted guard cells (Blevins and Lukaszewski 1998; Huang et al. 2000). Male sterility develops in the anther at < 9 mg B kg⁻¹ dry weight), while the carpel is affected only when B levels drop < 6 mg kg⁻¹ dry weight (Rerkasem et al. 1997).

2.6 Boron concentrations and requirements in plant parts

The requirements and responses of plants to applied B vary among plant species (Rashid et al. 2002c). Dicots have a higher internal B requirement, 4–7 times higher (20–70 mg kg⁻¹) than monocots (5–10 mg kg⁻¹) (Marschner 1995), due to differences in cell wall composition and extensibility due to level of pectin (Hu et al. 1996). Grasses have small amounts of pectin in the primary cell wall (Darvill et al. 1980) and thus require less B (only 3–10 µg g⁻¹ dry weight) (Jones et al. 1991) than dicots with more pectin (Darvill et al. 1980) and greater tissue B requirements (20–30 µg g⁻¹) (Jones et al. 1991). In monocots, including rice, the B requirement for reproductive and vegetative growth is relatively high; for normal pollen and grain development, anthers require > 20 mg kg⁻¹ compared to 3 mg kg⁻¹ in the flag leaf (Lordkaew et al. 2013). Below this concentration, significant reductions in reproductive and vegetative growth occur (Lordkaew et al. 2013). In Pakistan, rice responded positively to 0.5–1.0 kg B ha⁻¹ applied at panicle initiation (Shah et al. 2011).

3 Boron in soil and its dynamics in rice production systems

Minerals and rocks are an important source of B in soils. However, the B sorbed on surfaces of clay, hydrous iron, aluminum oxides, and organic matter has a more direct effect on plant-available B (Xu et al. 2001). In soil, B is present in (i) water-soluble forms, (ii) nonspecifically and specifically adsorbed forms, (iii) Fe–Al and Mn oxide-bound forms, and (iv) residual B fractions (Xu et al. 2001). Boron distribution and its transformations vary among different soil types, soil amendments, and management practices, which affect the availability of B to plants (Xu et al. 2001). The B concentration in soils ranges from 2 to 200 mg kg⁻¹, but < 5–10% of total B is available to plants (Diana 2006), of which a trace to 0.34% is in water-soluble, nonspecifically adsorbed or exchangeable forms (0–0.23%) and specifically adsorbed or nonexchangeable forms (0.05–0.30%) (Jin et al. 1987). In another study of B forms, freely soluble and specifically adsorbed B comprised < 2% of total B, while B sorbed on different oxides and hydroxides was 2.3% of total B (Hou et al. 1994). Boric acid (H₃BO₃) and borate (B(OH)₄⁻) are the only forms of soil B that are directly absorbed by plants. Boric acid is the predominant form commonly occurring at pH 4–9, while H₂BO₃⁻ is a significant form above pH 8 (Gupta 1979). Adsorbed B is the main source of soluble B in the soil solution. Adsorbed B mainly occurs as complexes of molecular boric acid or hydrated borate ions with broken Si–O and Al–O bonds at the edge of aluminosilicate minerals,

amorphous Al–Si oxide structures, magnesium hydroxide clusters, and Fe and Al oxyhydroxides. Adsorbed B present on noncrystalline or crystalline Al and Fe oxyhydroxides and silicates or adsorbed on clay particles is available to plants to some extent (Jin et al. 1987). The amount of B released to the soil solution during mineral weathering interacts primarily with Fe and Al hydroxides, Fe(OH)₃ and Al(OH)₃, respectively, and increases with increasing pH from 7 to 9 (Isirimah et al. 2003). With increasing pH (maximum pH 9), B adsorption increases and starts decreasing with further increase in pH > 9 (Goldberg 1997; Goldberg et al. 2005).

Boron adsorbed on the surface of freshly precipitated Al(OH)₃ is slowly released over time in flooded rice fields (Yu and Bell 2002). The formation of amorphous Fe oxyhydroxides as flooded soils, drained and oxidized, may increase the sorption of soluble B. Due to the water scarcity in Asia, rice cultivation is shifting from the puddled-transplanted system to water-saving production systems such as aerobic culture. In these systems, the availability of B to rice plants changes; the possible implications for this are discussed below.

3.1 Flooded rice system

In Asia, about 70% of rice is cultivated in standing water following transplantation of nursery-raised seedlings in puddled soil. In this system, the soil remains saturated with 7–10-cm standing water from sowing to maturity (Farooq et al. 2007a; Bouman and Tuong 2001). During this period, soils undergo physical, chemical, and biochemical changes (De Datta 1981), such as depletion of oxygen, decreased redox potential, increased pH in acidic soils, and decreased pH in alkaline soils (Renkou et al. 2003). The decreases in redox potential reduce Fe³⁺ to Fe²⁺ which increases the solubility of a range of important soil minerals.

Boron deficiency is considered an important nutritional disorder in flooded lowland rice grown in calcareous soils, limiting its productivity (Rashid et al. 2004, 2007). Boron deficiency in rice mainly results from low soil organic matter content, strong adsorption of B on soil particles and leaching losses (Rashid et al. 2007; Saleem et al. 2011a) due to high water percolation in paddy fields (Saleem et al. 2011b). Undissociated boric acid and borate anions move freely in water and readily leach from the upper soil layer. In flooded soils, B availability decreases in acidic soils due to its high mobility and, therefore, leaching (Katyal and Singh 1992). Fixation of added B through adsorption occurs in soils with high clay contents (Bhatnagar et al. 1979; Mezuman and Keren 1981; Elrashidi and O'Connor 1982).

Boron availability to plants declines at high pH levels due to its greater adsorption (Gupta 1993; Goldberg 1997); a negative interaction between soil pH and plant B occurs at pH > 6.3 (Peterson and Newman 1976), which is common in

puddled rice fields (Yu and Bell 2002). Boron uptake was four times higher at pH 4 than pH 9 (Sprague 1972); moreover, soil pH significantly affected the adsorption of B by soil particles, increasing over the pH range 3–9 (Keren et al. 1985; Lehto 1995; Mezuman and Keren 1981; Goldberg 1997), but decreasing over the pH range 9–11.5 (Goldberg and Glaubig 1986). A change in soil pH after soils are flooded induces changes in the dynamics of B (Yu and Bell 2002). Two factors are responsible for low B absorption at high soil pH (Keren and Bingham 1985): (1) at $\text{pH} < 7$, $\text{B}(\text{OH})_3$ dominates and the amount of B adsorption by the soil becomes small due to less fixation, and (2) as pH increases above 7.5, $\text{B}(\text{OH})_4^-$ becomes increasingly prevalent and clay minerals have a relatively strong affinity for $\text{B}(\text{OH})_4^-$, which increases its adsorption by soil particles (Keren and Bingham 1985). Fine-textured soils retain B longer than coarse-textured soils due to their higher adsorption affinity (Gupta 1968; Goldberg and Glaubig 1986; Nicholaichuk et al. 1988; Butterwick et al. 1989). Rice cultivated in coarse-textured soils faces B deficiency due to high leaching losses.

3.2 Aerobic rice system

An aerobic rice production system is a water-saving technology, characterized by sowing rice in aerobic field conditions directly from seed rather than by seedling transplantation (Bouman et al. 2005; Prasad 2011). The aerobic system is practiced in Asian countries including China, India, Bangladesh, Sri Lanka, Nepal, Pakistan, and Bhutan; Southeast Asian countries including the Philippines, Vietnam, and Thailand; and African and Latin America countries (Gupta and O'Toole 1986; Gao et al. 2012). In some regions, B deficiency is observed in rice established through this system (Rehman et al. 2016) due to reduced moisture contents which decrease B mobility to plant roots.

Boron availability changes in aerobic rice culture due to fluctuating soil pH (Liu 1996) and higher redox potential (Gao et al. 2002), resulting in the oxidation of Fe or Mn and adsorption of B by their oxyhydroxides. In aerobic soils, nitrification increases and plants take up N as NO_3^- instead of NH_4^+ . As a result, the OH^- concentration increases in the rhizosphere and the increase in pH may lead to reduced B availability (Gao et al. 2006). Furthermore, B availability decreases in dry soils making its deficiency more likely, because drying reduces its mobility to plant roots and restricts the ability of plants to take up B from the soil (Sulaiman and Kay 1972).

4 Factors affecting boron availability in rice

Various factors such as high pH, alkalinity, inadequate soil organic matter, soil adsorptive capacity, amounts and types

of minerals in the soil, soil water contents, and leaching, particularly in coarse-textured soils, affect the availability of B to plants (Goldberg 1997) and are described below.

4.1 Soil characteristics

4.1.1 Soil pH

Soil pH is the most important factor affecting B availability. Soluble B content ($0.10\text{--}0.45 \mu\text{g g}^{-1}$) in soils is negatively correlated with soil solution pH (Niaz et al. 2007). Boron uptake by plants at optimum water-soluble B levels is higher at lower soil solution pH (Wear and Patterson 1962). Therefore, an increasing soil solution pH will generally decrease B availability to plant roots, resulting in severe B deficiency in rice crops, particularly in calcareous soils (Rashid 2006). Soil adsorptive capacity increases at pH corresponding to the pK_a of boric acid, i.e., nearly 9.1 (Schalscha et al. 1973).

4.1.2 Soil salinity

Rice grown in saline soils and/or with high-sodium irrigation water experienced B deficiency due to a negative interaction between soil B availability and a high sodium adsorption ratio (SAR) (Wimmer et al. 2003; Masood et al. 2012). However, with increasing salinity, the effects of excessive B are substantially reduced (Yermiyahu et al. 2008). Ismail (2003) indicated an additive effect of high B and salinity, whereas some researchers reported no interaction for shoot B concentration (Wimmer et al. 2003). It has been reported that salinity alleviated B toxicity by reducing shoot B concentration (Ismail 2003; Diaz and Grattan 2009). An increase in salt concentration can increase the B concentration in roots and leaves. Under saline conditions, B forms a complex with rhamnolacturonan in the cell walls which leads to a reduction in cell wall pore size (Brown et al. 2002). Some studies have observed B toxicity in salt-prone calcareous soils, but none were with rice (Sillanpaa 1982; Yau 1997). Boron deficiency has also been observed in rice grown in saline soils in Pakistan (Aslam et al. 2002).

4.1.3 Soil organic matter

Organic matter is a store for soil nutrients including B and is thus an important constituent affecting B availability to plants (Goldberg 1997). Various studies have described a significant correlation between soil B availability and soil organic carbon (Elrashidi and O'Connor 1982; Goldberg 1997; Keren et al. 1985). Boron may be adsorbed with organic matter or with carbohydrate release during humification; in most agricultural soils, B associated with humic colloids acts as principal B pool for plant growth (Jones 2003). In Pakistan, low soil organic matter is considered a major factor responsible for B

deficiency (Rashid et al. 2002c). Organic matter contents vary among different rice production systems. For instance, under aerobic rice production, organic matter decomposes at a faster rate than anaerobic systems (Sahrawat 2005). The slow decomposition of organic matter in submerged conditions leads to its accumulation in the soil (Sahrawat 2005). Wetland rice production sequesters about 11–20% more C than aerobic rice production (Witt et al. 2000), increasing soil fertility, which is considered a mainstay for the long-term sustainability of this system. Humus also contains significant amounts of B (Parks and White 1952), but adsorption of B is higher with organic matter than clay minerals on weight basis (Yermiyahu et al. 1988; Gu and Lowe 1990) and increases with the addition of composted organic matter (Yermiyahu et al. 1995). Boron adsorption to organic matter is affected by soil pH; at low pH, adsorption of B to organic matter is very low (Okazaki and Chao 1968). Boron forms diol complexes with decomposed organic matter (Parks and White 1952); α -hydroxycarboxylic acid may act in B sorption on organic matter (Huettl 1976). Boron adsorbed to organic matter has decreased availability through the ligand exchange mechanism (Yermiyahu et al. 1988).

4.1.4 Soil adsorption

Several factors can affect B adsorption including the concentration of B in the soil, soil texture and structure, organic matter, soil pH, cation exchange capacity, exchangeable ion composition, and the type and amount of clay (Bingham 1973). When B is released from different sources, such as minerals, organic matter, or added fertilizers, some becomes available to plants while a significant amount is adsorbed by soil particles (Gupta 1979). Various studies have reported that soil adsorption generally occurs on the aluminosilicate clay minerals (Jasmund and Lindner 1973; Keren and Talpaz 1984; Mattigod et al. 1985). Boron in soluble and adsorbed forms remains in equilibrium (Bingham 1973). More B is present in the adsorbed form than in soil solution (Jame et al. 1982) which may increase with time (Gupta 1968). Among aluminosilicate clay minerals, illite is considered the most reactive with B, while kaolinite is the least reactive (Keren and Mezuman 1981).

4.2 Interaction with other nutrients

Boron interacts with other mineral elements present in soil (Bonilla et al. 2004; Tariq and Mott 2007). Hence, the availability of B to plants is influenced by the concentrations of other nutrient elements in the growing media as discussed below.

4.2.1 Nitrogen

Nitrogen affects the availability of B to plants. Generally, N has a negative interaction with B (Jones et al. 1963); therefore, N application helps to reduce B toxicity (Chapman and Vaselow 1955), but its beneficial effect depends on the plant species and N rate. Under greenhouse conditions, the application of N significantly decreased B toxicity in rice (Koohkan and Maftoun 2015). Another study indicated that N concentration alleviates the severity of B toxicity symptoms (Gupta et al. 1973). Adding N fertilizers to N-deficient soils substantially decreases B concentration of boot stage tissue of cereals that helps in mitigating its toxicity problem (Gupta et al. 1973). However, increasing N application may increase the intensity of deficiency symptoms (Tanaka 1967). Boron availability in soil solution increases because nitrates inhibit B sorption with Fe and Al oxides (Abbas et al. 2013). Moreover, crop biomass improved when N was applied with B (Smithson and Heathcote 1976).

4.2.2 Phosphorus

The association of B with phosphorus (P) is less clear (Gupta 1979). Borate resembles phosphate in its physiological and biochemical actions. Like P, borates are components of physiologically active esters and form polyhydroxyl compounds with some organic complexes (Bergmann 1992). However, the uptake and transport of B into plants is interrelated with P uptake (Günes and Alpaslan 2000). Under B-deficient conditions, the rate of phosphate uptake decreases but is restored upon B application (Robertson and Loughman 1974). Phosphorus deficiency symptoms become more severe under B-deficient conditions (Chatterjee et al. 1990). Like N, P is helpful in alleviating the toxic effects of B in calcareous soils. In calcareous soils, where B levels become toxic in P deficiency situations, the addition of P helps to decrease B toxicity (Günes and Alpaslan 2000).

4.2.3 Potassium

The nature of the complex relationship between B and potassium (K) is unclear (Samet et al. 2015). Boron may enhance stomatal opening by affecting K^+ efflux of guard cells in epidermal strips (Roth-Bejerano and Itai 1981). At low B levels, an increase in K fertilization may accentuate B deficiency symptoms. However, under high B supply, high rates of K may increase the uptake of B (Huang and Snapp 2009). Accentuated B deficiency and toxicity symptoms by high K application might be due to the effect of K on cell permeability that is controlled by B (Gupta 1979). Potassium indirectly influences B availability due to its effect on Ca absorption, because Ca clays adsorbed more B than K clays (Mattigod et al. 1985). Nonetheless, excessive B application augmented

both B and K concentrations in rice plants (Kumar et al. 1981), because optimal B level increases K permeability in cell membrane (Schon et al. 1990).

Under severe B deficiency, the net efflux from leaves was 35-fold higher for K^+ , 45-fold higher for sucrose, and 7-fold higher for phenolics and amino acids than those that were nondeficient in B (Cakmak and Römheld 1997). Furthermore, B application increases the B and K concentrations, as observed in rice (Kumar et al. 1981).

4.2.4 Calcium

Calcium (Ca) as a component of lime affects B availability (Eck and Campbell 1962). A positive relationship between B and Ca is well established (Tisdale et al. 1985; Bonilla et al. 2004). In alkaline and excessively limed soils, free Ca ions restrict B availability and protect plants from the toxic effect of excess B (Tisdale et al. 1985). Calcium reduces the availability of B, possibly due to the formation of a calcium metaborate complex in soil (Sillanpää 1972). Ca^{2+} ions help in maintaining the integrity of the cell wall due to its role in B-diester bonds in the pectate layer (Matoh and Kobayashi 1998). The ratio between Ca and B in leaf tissue is used as a parameter for assessing B status in crops (Tisdale et al. 1985).

4.3 Environmental factors

Various environmental factors, including light intensity and relative humidity, affect nutrient dynamics. Environmental factors that affect B availability, uptake, and requirements by plants are discussed below.

4.3.1 Light intensity

Plants grown under high light intensity require more B for leaf growth than plants grown under low light intensity. In summer months, with high light intensity and long photoperiods, B deficiency symptoms are enhanced in plants leading to speculation that exposure to high light intensity increases B requirements in plants (Warington 1933). Moreover, high light intensity increases plant sensitivity to B deficiency (Cakmak and Römheld 1997). A significant decrease in B uptake rate and translocation from roots to shoots and its partitioning into actively growing young leaves has been reported under high light situations (midday photon flux density 1500–2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Ye 2005). Under low light conditions, less B is required for leaf blade elongation (Cakmak and Römheld 1997). High light intensity and low temperature are important factors that need to be considered in relation to the occurrence of B deficiency (Shorrocks 1997). The increase in B demand under high light intensity results from stimulated young leaf growth but increased transpiration by old leaves

that shifted the B partitioning away from the growing tissues that have highest B demand (Huang et al. 2001).

Light intensity plays a major role in B deficiency-induced K^+ leakage (Cakmak and Römheld 1997). Marschner (1995) reported that, in B-deficient plants, the activity of polyphenol oxidase (PPO) in leaf extracts progressively increased with severity of B deficiency symptoms, particularly under high light intensity. Boron deficiency is associated with enhanced browning of leaf tissues, which is a consequence of enhanced phenol accumulation and PPO activity.

4.3.2 Relative humidity

Relative humidity also affects B concentrations in plants (Gupta 1979). Bowen (1972) reported that in sugarcane, B concentrations decreased from 16.5 to 9.9 mg B per plant as relative humidity increased from 30 to 90%; the decrease in relative humidity also increased B absorption. Hu and Brown (1997) described relative humidity as one of the main environmental factors affecting B availability. Under low relative humidity, transpiration increases which triggers B uptake (Hu and Brown 1997). A strong relationship between relative humidity and transpiration rate may explain why B-induced sterility in wheat is accentuated by under humid conditions during pollen development (Rawson 1996). Low temperature might increase the plant B demand; besides, the reduction of B uptake by plant roots or low B tissues may be more susceptible to chilling damage than optimal B tissues (Ye 2004). Low root temperature (10–17 °C) causes substantial reduction in plant B uptake efficiency and utilization of B in the shoot (Huang et al. 2005).

4.4 Boron interaction with soil biota

Boron is involved in symbiotic N fixation in legumes (Brenchley and Thornton 1925). Boron modulates the growth of infection threads and nodule invasion by regulating the connections between plant roots, infection thread matrix glycoproteins, and the bacterial cell surface (Bolaños et al. 2004). The peribacteroid membrane surrounding the bacteroid in nodule cells controls nutrient transport between rhizobia and roots (Cakmak and Römheld 1997). Boron regulates the cross-linking of cell wall components and imparts strength to the peribacteroid membrane; glycocalyx rich in *cis*-diol groups is also a candidate for borate cross-linking. The glycoproteins attach to the cell surface of rhizobia in the absence of B. As a result, the bacteria intermingle with the root cell membrane which inhibits the endocytosis process, resulting in failed cell invasion (Cakmak and Römheld 1997). Boron stabilizes membranes, which facilitates the association between bacterial cell surfaces and the peribacteroid membranes, which then regulate symbiotic establishment (Bolaños et al. 1996). The B-containing bacterial signal molecule

(autoinducer AI-2) has been recently discovered; the addition of naturally occurring borate to AI-2 precursor generates active AI-2 that indicates its potential biological role for B (Chen et al. 2002). The AI-2 molecule is a furanosyl borate-diester that acts as a novel signaling molecule for bacterial structure and function. It is formed by most bacteria and is not exclusive to a single species. The gene encoding AI-2 synthase (*luxS*) is broadly preserved, and it is possible that AI-2 will be a universal bacterial signal for communication among species (Chen et al. 2002). It may be used as a B transporter depending on growth or environmental conditions (Coulthurst et al. 2002).

Boron deficiency may also affect mycorrhizal development due to poor root development and decreased transport of carbohydrate to roots. Under B fertilization, the development of endomycorrhizae in roots occurs due to the activity of indole 3-acetic acid (IAA) oxidase activity that triggers IAA levels—ultimately enhancing the transport of carbohydrates to roots (Patrick and Wareing 1973; Lambert et al. 1980). Boron deficiency adversely affects the fungi–mycorrhizal interaction resulting in decreased transport of carbohydrates (Middleton et al. 1978) to plant roots by altering IAA oxidase and auxin levels (Van de Vender and Currier 1977). Mycorrhiza (*Glomus clarum*) inoculation helps to reduce B toxicity by decreasing shoot B concentration (Sonmez et al. 2009).

5 Diagnosing boron deficiency in rice

Boron is an essential nutrient with a key role in improving rice crop growth and development. Therefore, the correct diagnosis of B deficiency is essential before attempting any corrective measures. Various approaches including visual deficiency symptoms, soil testing, and plant analysis can be employed to diagnose B deficiency. Additionally, knowledge about the soil and other factors known to accentuate B deficiency can help in the effective diagnosis of its deficiency.

Immobility of B in most plant species causes B deficiency symptoms that first appear in young plant parts including apices, flowers, fruits, and seeds (Fig. 1). The most frequent B deficiency symptoms include flower bud abortion, sterile male flowers, reduced seed size, and impaired fruit quality (Fig. 1; Dell and Huang 1997). In Pakistan, B deficiency delays flowering in rice by 4 days (Rashid et al. 2000). Moreover, B deficiency induces sterility in the lower panicles of rice (Rashid 2006; Rashid et al. 2007). Under B deficiency, chlorophyll contents in rice plants decrease due to the inhibition of photosynthesis and poor development of chloroplasts (Wang et al. 2007).

In Pakistan, the dilute HCl (i.e., 0.05 M HCl) method, originally used to determine B availability in acid rice soils, is equally effective for predicting B deficiency in alkaline and

calcareous soils (Kausar et al. 1990; Rashid et al. 1994, 1997). Critical concentrations for predicting B deficiency by plant analysis in some important crops in rice-based cropping systems are given in Table 1.

6 Managing boron deficiency in rice

Boron application to rice production systems (aerobic and flooded) on low B soils improves yields and ameliorates B deficiency. However, the effectiveness of different application methods and sources of B may vary. Strategies for improving yields and grain quality in rice through B application are discussed below.

6.1 Yield and grain quality enhancement with boron fertilization

Historically, rice crops were considered tolerant to B deficiency (Lucas and Knezek 1972; Savithri et al. 1999). However, recent research has revealed that B deficiency in rice soils is an important reason for low kernel yields (Rashid et al. 2004, 2007). Dunn et al. (2005) reported that the use of B fertilizer in rice substantially improved yield. In the 1970s, in Pakistan (Punjab), the application of B fertilizer in farmers' fields improved rice yields (cvs. Basmati-370, IR-6) by 14%. However, the B status of the soils and rice plants was not reported until 1967 (Chaudhry et al. 1976). Field experiments across multiple locations and years in rice-growing areas of Punjab, Pakistan, in low B calcareous soils (0.21–0.42 mg B kg⁻¹) with low organic matter (0.8–1.8%) revealed B deficiency as a widespread nutritional problem (Rashid et al. 2004, 2007). Boron fertilization (1.0 kg B ha⁻¹) improved paddy yields in several rice genotypes (Super Basmati, Basmati-385, KS-282; Table 2), which was attributed to reduced panicle sterility and an increased number of productive tillers (Rashid et al. 2004, 2007). Boron fertilizer use (0.75 kg B ha⁻¹) reduces panicle sterility and increases productive tillers, which result in higher paddy yields (Rashid et al. 2004, 2007).

Boron fertilization in deficient soils not only enhances crop yield but also improves rice grain quality (Rehman et al. 2014a). Soil-applied B increased milling return along with head rice recovery and grain and cooking characteristics. Moreover, it improved the desirable cooking quality traits such as quality index, kernel elongation ratio and bursting (upon cooking), and alkaline spreading value (Table 3). Improved cooking quality in rice with B nutrition was attributed to better grain filling (Rashid et al. 2004, 2007). Thus, adequate B nutrition of rice plants appears to be a prerequisite for obtaining optimum yields and quality rice.

Table 1 Boron deficiency critical concentration/range of some common crops in rice-based cropping systems

Crop species	Plant part and growth stage	Deficiency critical concentration/range (mg B kg ⁻¹)	Source
Rice	Flag leaves ¹	6	Jones Jr et al. (1991), Reuter et al. (1997)
Wheat	Whole shoots (≤ 30 cm tall)	4–6	Rashid et al. (2002a)
	Youngest mature leaves	5–7	
Rapeseed	Whole shoots (≤ 30 cm tall)	32	Rashid et al. (2002b)
	Youngest mature leaves ¹	38	
Soybean	Youngest mature leaves ¹	25	Small and Ohlrogge (1973), Weir and Cresswell (1994)
	Youngest mature leaves ¹	20	

¹ Youngest fully expanded leaf blades at flowering/heading

6.2 Boron fertilization

Boron is used in small amounts as a micronutrient either alone or within macronutrient fertilizers. The B requirement varies from crop to crop. Since in most plants, it is not easily retranslocated, B should be continuously available for uptake by plant roots. Therefore, the selection of a suitable B source is imperative for improving the B status in rice crops. Different B sources and application methods are discussed below.

6.2.1 Sources of boron

Boron fertilizer sources are categorized into (i) completely refined soluble materials, which may be solid or in solution, such as borax (Na₂B₄O₇·10H₂O), boric acid (H₃BO₃), sodium tetraborate (Na₂B₄O₇·5H₂O), sodium pentaborate (Na₂B₁₀O₁₆·10H₂O), and *Solubor* (Na₂B₈O₁₃·4H₂O); and (ii) crushed minerals including ascharite (2MgO·B₂O₃·H₂O), colemanite (Ca₂B₆O₁₁·5H₂O), datolite (2CaO·B₂O₃·2SiO₂·H₂O), hydroboracite (CaO·MgO·3B₂O₃·6H₂O), and ulexite (Na₂

Table 2 Paddy yield, agronomic traits, plant B concentration and uptake, and B use efficiency as affected by B application in calcareous soils of Pakistan

Cultivar	B applied (kg ha ⁻¹)	Paddy yield (t ha ⁻¹)		Panicle sterility (%)	Productive tillers hill ⁻¹	B concentration (mg kg ⁻¹)		B uptake (g ha ⁻¹)	B use efficiency (%)
		Paddy	Straw			Leaves	Paddy		
2002 (5 field locations)									
Super Basmati	0	3.23	5.15a	23a	18.4	5.5a	1.73a	17.2a	1.68
	1	3.89	5.88b	14b	20.1	8.5a	2.51b	34.0b	
	LSD (0.05)	0.68	0.41	4	NS	0.6	0.29	1.4	
Basmati-385	0	3.77a	5.43a	28a	14.3	5.3a	1.33a	17.4a	1.78
	1	4.72b	6.63b	16b	16.1	8.2b	2.49b	35.2b	
	LSD (0.05)	0.45	0.29	8	NS	0.5	0.18	1.5	
2003 (6 field locations)									
Super Basmati	0	3.78b	9.74b	18a	19b	7.2b	1.60b	31.1b	3.10
	1	4.39a	11.30a	12b	22a	9.3a	2.74a	61.7a	
	LSD (0.05)	0.60	0.36	6	3	1.3	0.24	12.9	
Basmati-385	0	3.69b	9.46b	24a	16b	7.2b	1.63b	29.2b	—
	1	4.54a	10.86a	19b	19a	8.8a	2.60a	57.1a	
	LSD (0.05)	0.79	0.87	5	2	1.0	0.20	13.7	
KS-282	0	4.82b	12.17b	15a	12b	6.9b	1.69b	35.4b	3.40
	1	5.48a	13.30a	12b	15a	8.3a	2.58a	69.6a	
	LSD (0.05)	0.64	0.94	5	2	1.2	0.08	8.9	

Source: Rashid et al. (2007). Means not sharing the same letter, for a parameter, variety and year, differ significantly at p≤0.05

Table 3 Influence of boron application on rice (cv. Super Basmati) grain and cooking quality

Grain characteristic	Boron applied (kg ha ⁻¹)				LSD (0.05)
	0.0	0.5	1.0	1.5	
Total milled rice (%)	70.4c	71.6b	72.3a	71.7b	0.5
Head rice (%)	51.6c	54.6b	57.0a	56.4a	0.6
Quality index	2.96b	2.96b	3.0a	2.97b	0.03
Elongation ratio upon cooking	1.88d	1.94c	2.00a	1.98b	0.02
Bursting-upon-cooking (%)	9.9a	9.0b	8.0c	8.4c	0.5
Alkali spreading value (score 1–7) ¹	4.5c	4.8b	4.9a	4.8b	0.1

Source: Rashid et al. (2004, 2007). Means followed by different letters are statistically different at LSD (0.05)

¹ Alkali spreading value: 4–5 score = intermediate G.T. type rice

O-2CaO·5B₂O₃·16H₂O) (Bell and Dell 2008). The solubility and efficiency of these sources in different rice production systems varies from soil to soil, but in B-deficient situations, B fertilizer has a positive effect on rice growth and productivity (Saleem et al. 2013). Boron fertilizer properties—such as dissolution kinetics, the ability to leach from the soil column—have a strong effect on B use efficiency (Saleem et al. 2009). For instance, sodium pentaborate and boric acid dissolve in soil solution to become readily available to plant roots. Similarly, powder colemanite increases rice growth more than granular colemanite due to the enhanced release of B (Saleem et al. 2013). Generally, ulexite and colemanite are applied to the soil in different production systems due to their long retention in the root zone (Bell and Dell 2008). The application of borax and colemanite in powder and granular forms improved rice yields in flooded conditions; however, borax was considered more efficient than other B sources (Saleem et al. 2011a) (Table 4).

6.2.2 Boron application methods

Foliar and soil application are common but often costly methods for micronutrient addition. Foliar fertilization alone may not fulfill the long-term demand of crops and should be considered a supplementary approach to soil application (Bell and Dell 2008). Different B application methods to correct deficiencies in rice-based systems are discussed below.

Soil application Soil application of B is the best strategy to ameliorate its deficiency. Soil B application rates for various crops and soils range from 0.25 to 3 kg B ha⁻¹ depending on soil type, crop requirement, and application method (Gupta 1979). There is a narrow range between B deficiency and toxicity; cereals including rice are B sensitive and show toxicity symptoms when grown on calcareous soils containing high levels of inherent B (Singh et al. 1990). Therefore, care needs to be taken in the application of a safe B dosage and uniform field broadcasts of B fertilizer. In transplanted rice, 0.75 kg B ha⁻¹ applied via broadcasting in calcareous soils

overcame its deficiency; moreover, it had a beneficial residual effect for the three subsequent crops grown in the same field (Rashid et al. 2007). The residual effect of B fertilizer depends on the soil type (Khan et al. 2011). For instance, in coarse-textured soils that are prone to leaching due to large pore spaces, the application of 1–2 kg B ha⁻¹ had little residual effect for the next crop/season. Soil B application as boric acid was retained for a short period and its availability ranged from 0.4 to 13.5% depending on the soil type (Jin et al. 1988). By contrast, on a range of soils in southeast China, 2.5–11% of the added B fertilizer was accounted for after 2–3 years by increases in hot CaCl₂-extractable B in the 0–20-cm layer (Wang et al. 1999). During that period, approximately 200 g B ha⁻¹ year⁻¹ or the equivalent of 2 kg borax ha⁻¹ year⁻¹ was removed in harvested products of oilseed rape and rice. After 3 years, crop removal accounted for 40% of 1.65 kg B ha⁻¹ applied, while the remainder was recovered in hot CaCl₂-extractable B in the 0–40-cm layer of the soil profile. Hence, the residual effects of B fertilizer applied to soil may vary considerably between rice-based cropping systems.

Foliar application Foliar B application is an effective strategy for improving B supply to plants especially when root growth is restricted due to dry soil conditions. However, B translocation from leaves to fruits or other parts varies among plant species. Foliar-applied B is readily retranslocated in plants that contain polyols such as sorbitol or mannitol in the phloem (Brown and Shelp 1997). Such compounds contain *cis*-diol moieties that complex with B in the phloem and ensure free movement from source to sink tissues. Otherwise, when B is immobile in the phloem, a single foliar spray of B was not sufficient. Repeated sprays can effectively sustain B supply to improve flowering (Wang et al. 1999). With foliar application, a low concentration of B is applied to avoid toxic effects (Shorrocks 1997) (Table 5).

Priming/coating strategies Seed priming is an effective approach for improving rice productivity by enhancing

Table 4 Comparative performance of soil-applied different B sources as basal fertilizer in different soil types and rice production systems

B sources	Application rate (kg B ha ⁻¹)	Time of application	Production system	Soil texture	Soil pH	Increase in grain yield over control (%)	Increase in B concentration in grain (paddy)/straw over control (%)	Leaf B concentration (m kg ⁻¹)	Country	Reference
Na ₂ B ₄ O ₇ ·10H ₂ O	5.6	At transplanting	Flooding, field trial at 20 locations	Clayey	7.5–8.5	10–35 (mean 14)	–	–	Pakistan	Chaudhry et al. (1976)
H ₃ BO ₃	4.4	At transplanting	Flooding in pot	Silt loam	4.8	11	–	11.3 (7.1)*	USA	Yu and Bell (2002)
Na ₂ B ₄ O ₇ ·5H ₂ O	1.12	Basal dose	Direct seeding in aerobic culture	Silt loam	6.3	0	–	6.3 (6.1)	USA	Slaton et al. (2004)
Na ₂ B ₄ O ₇ ·5H ₂ O	2.24	Basal dose	Direct seeding in aerobic culture	Silt loam	6.3	2	–	6.4 (6.1)	USA	Slaton et al. (2004)
Na ₂ B ₄ O ₇ ·5H ₂ O	4.48 ¹	Basal dose	Direct seeding in aerobic culture	Silt loam	6.3	0	–	6.2 (6.1)	USA	Slaton et al. (2004)
Na ₂ B ₄ O ₇ ·5H ₂ O	6.73 ¹	Basal dose	Direct seeding in aerobic culture	Silt loam	6.3	0	–	7.2 (6.1)	USA	Slaton et al. (2004)
Na ₂ B ₄ O ₇ ·10H ₂ O	8.97 ¹	Basal dose	Direct seeding in aerobic culture	Silt loam	6.3	0	–	7.2 (6.1)	USA	Slaton et al. (2004)
Na ₂ B ₄ O ₇ ·10H ₂ O	1.00	At transplanting	Conventional flooding	Silt loam	7.9–8.8	25	–	8.2 (5.3)	Pakistan	Rashid et al. (2004)
H ₃ BO ₃	0.28–3.54	At transplanting	Conventional flooding	Sandy clay loam	7.8	0–37	1–13 in straw	–	Pakistan	Shafiq and Maqsood (2010)
Na ₂ B ₄ O ₇ ·10H ₂ O	1.00	At transplanting	Conventional flooding	–	7.4–8.4	31	–	–	Pakistan	Ahmad and Irshad (2011)
Na ₂ B ₄ O ₇ ·10H ₂ O	1.00–3.00	At transplanting	Conventional flooding	Silty clay loam	7.0	17–28	56–89 in grain	–	Malaysia	Saleem et al. (2011b)
Ca ₂ B ₆ O ₁₁ ·5H ₂ O (powder)	1.00–3.00	At transplanting	Conventional flooding	Silty clay loam	7.0	17–24	41–74 in grain	–	Malaysia	Saleem et al. (2011b)
Ca ₂ B ₆ O ₁₁ ·5H ₂ O (granular)	1.00–3.00	At transplanting	Conventional flooding	Silty clay loam	7.0	3–10	8–30 in grain	–	Malaysia	Saleem et al. (2011b)
H ₃ BO ₃	0.50–0.75	At transplanting	Conventional flooding	Clay loam	7.7	8–17	–	–	Pakistan	Shah et al. (2011)
Na ₂ B ₄ O ₇ ·10H ₂ O	1.50	At transplanting	Conventional flooding	Silty clay	8.0	13	–	–	Pakistan	Hussain et al. (2012)
Na ₂ B ₄ O ₇ ·10H ₂ O	1.50	At tillering	Conventional flooding	Silty clay	8.0	14	–	–	Pakistan	Hussain et al. (2012)
Na ₂ B ₄ O ₇ ·10H ₂ O	1.50	At flowering	Conventional flooding	Silty clay	8.0	20	–	–	Pakistan	Hussain et al. (2012)
Na ₂ B ₄ O ₇ ·10H ₂ O	1.50	At grain formation	Conventional flooding	Silty clay	8.0	14	–	–	Pakistan	Hussain et al. (2012)
H ₃ BO ₃	2.00	At transplanting	Conventional flooding	Clay	8.11	53	–	–	Pakistan	Abbas et al. (2013)
Ca ₂ B ₆ O ₁₁ ·5H ₂ O (powder)	1.00–3.00	At transplanting	Conventional flooding	Silty clay	8.10	5–21	17–67 in grain	–	Malaysia	Saleem et al. (2013)

Table 4 (continued)

B sources	Application rate (kg B ha ⁻¹)	Time of application	Production system	Soil texture	Soil pH	Increase in grain yield over control (%)	Increase in B concentration in grain (paddy)/straw over control (%)	Leaf B concentration (m kg ⁻¹)	Country	Reference
Ca ₂ B ₆ O ₁₁ ·5H ₂ O (granular)	1.00–3.00	At transplanting	Conventional flooding	Silty clay	8.10	2–9	12–23 in grain	–	Malaysia	Saleem et al. (2013)
H ₃ BO ₃	1.00	Basal dose	Direct seeding in aerobic culture	Sandy loam	8.2	19–42	32–43 in grain	–	Pakistan	Rehman et al. (2014a, 2016)
H ₃ BO ₃	1.00	At transplanting	Alternate wetting and drying	Sandy loam	8.2	9–11	37–48 in grain	–	Pakistan	Rehman et al. (2014a, 2016)
H ₃ BO ₃	1.00	At transplanting	Conventional flooding	Sandy loam	8.2	22–40	23–39 in grain	–	Pakistan	Rehman et al. (2014a, 2016)
H ₃ BO ₃	0.50–1.50	Basal dose	Direct seeding in pot	Sandy loam	8.2	7–26	3–37 in grain	–	Pakistan	Rehman et al. (2015)
Na ₂ B ₄ O ₇ ·10H ₂ O	7.50	Basal dose	Direct seeding in aerobic culture	Silt clay	7.9	11	–	–	Pakistan	Sarwar et al. (2016)
Na ₂ B ₄ O ₇ ·10H ₂ O	7.50	Basal dose	Alternate wetting and drying	Silt clay	7.9	3	–	–	Pakistan	Sarwar et al. (2016)
Na ₂ B ₄ O ₇ ·10H ₂ O	7.50	Basal dose	Conventional flooding	Silt clay	7.9	6	–	–	Pakistan	Sarwar et al. (2016)

*Values in parenthesis indicate leaf B contents in control treatment

Table 5 Comparative performance of different foliar-applied, seed-treated, and root-dipped B sources in various rice production systems

B source	Application method	Application rate	Production system	Soil texture	Soil pH	Increase in grain yield (paddy) over control (%)	Increase in B contents of grain over control (%)	Country	Reference
H ₃ BO ₃	Foliar application	200 mM	Alternate wetting and drying	Sandy loam	8.2	10–19	60–62	Pakistan	Rehman et al. (2014b, 2016)
H ₃ BO ₃	Foliar application	200 mM	Direct seeding in aerobic culture	Sandy loam	8.2	18–20	62–65	Pakistan	Rehman et al. (2014b, 2016)
H ₃ BO ₃	Foliar application	200 mM	Conventional flooding	Sandy loam	8.2	23–46	29–35	Pakistan	Rehman et al. (2014b, 2016)
Na ₂ B ₈ O ₁₃ ·4H ₂ O	Foliar application	1.12–8.97 kg ha ⁻¹	Direct seeding in aerobic culture	Silt loam	6.3	3	–	USA	Slaton et al. (2004)
H ₃ BO ₃	Foliar application	0.2–0.8 ppm	Conventional flooding	Clay	8.1	3–10	–	India	Rao et al. (2013)
H ₃ BO ₃	Foliar application	0.2–0.8 ppm	Conventional flooding	Sandy loam	4.6	20	–	India	Rao et al. (2013)
H ₃ BO ₃	Foliar application	0.2–0.8 ppm	Conventional flooding	Sandy silty	7.2	8–13	–	India	Rao et al. (2013)
H ₃ BO ₃	Foliar application	0.2–0.8 ppm	Conventional flooding	Silty loam	8.0	0	–	India	Rao et al. (2013)
H ₃ BO ₃	Foliar application	0.2–0.8 ppm	Conventional flooding	Sandy clay loam	6.8	4–9	–	India	Rao et al. (2013)
H ₃ BO ₃	Foliar application	0.2–0.8 ppm	Conventional flooding	Silty clay	5.5	3–4	–	India	Rao et al. (2013)
Na ₂ B ₄ O ₇ ·10H ₂ O	Foliar application	1.5% B solution	Conventional flooding	Silty clay	8.0	8–10	–	Pakistan	Hussain et al. (2012)
H ₃ BO ₃	Seed coating	1.0–3.0 g kg ⁻¹ of seed	Direct seeding in aerobic culture	Sandy loam	8.2	5–20	5–42	Pakistan	Rehman and Farooq (2013)
H ₃ BO ₃	Seed priming	0.001%, 0.01% B solution	Direct seeding in aerobic culture	Sandy loam	8.2	12–34	33–47	Pakistan	Rehman et al. (2012b)
H ₃ BO ₃	Seed priming	0.1 mM	Alternate wetting and drying	Sandy loam	8.2	16–17	36–41	Pakistan	Rehman et al. (2014b, 2016)
H ₃ BO ₃	Seed priming	0.1 mM	Conventional flooding	Sandy loam	8.2	18–27	26–36	Pakistan	Rehman et al. (2014b, 2016)
H ₃ BO ₃	Seed priming	0.1 mM	Direct seeding in aerobic culture	Sandy loam	8.2	11–15	31–43	Pakistan	Rehman et al. (2014b, 2016)
Na ₂ B ₄ O ₇ ·10H ₂ O	Seedling roots dipped in B solution	1.5% B solution	Conventional flooding	Silty clay	8.0	10	–	Pakistan	Hussain et al. (2012)

germination (Farooq et al. 2007a, b; Harris et al. 2002). Seed priming usually increases the germination rate and uniformity (Farooq et al. 2006a, b, c). Seed priming is an attractive technique, as it improves rice growth by improving different germination attributes (Farooq et al. 2011; Rehman et al. 2013). In rice, seed treatment with B improved radicle and plumule lengths as B plays a vital role in cell division, cell elongation, and primary events of germination (Shelp 1993). Boron seed priming enhances rice growth in different production systems, more so in aerobic rice (Rehman et al. 2014a, 2016). Seed coating is also effective for increasing B availability during initial plant growth stages. Seed coating of rice with B improved tillering (Rehman et al. 2012a), root and leaf scores, and the number of secondary roots (Farooq et al. 2011).

6.2.3 Residual effect of soil-applied boron fertilizer

Fertilizer B recovery is the fraction of B applied that is taken up by plants and translocated to the grain. Boron applied to the soil can result in a beneficial residual B for the succeeding crop(s), even at a rate of 1.0 kg B ha^{-1} (Yang et al. 2000). For example, only 1.7–3.4% (plant basis) of the applied B was taken up by transplanted rice grown in calcareous soils in Pakistan (Rashid et al. 2007). The removal of fertilizer B from the soil depends on the rice cultivar and its yield potential (Table 6; Rashid et al. 2007). In a rice–wheat system in Pakistan, rice yields increased by 25% with B application, and the residual B increased the yield of the succeeding wheat crop by 22–24% (Rashid, unpublished data). The magnitude of the beneficial residual effect of soil-applied B depends on many factors, such as soil properties influencing B adsorption/desorption and the leaching of B beyond the root zone. The overall crop demand, which can be high in intensive triple-cropping patterns, also determines how much B remains in the soil after 1 year (Wang et al. 1999). For example, B adsorption in fine-textured soils can result in a significant carryover effect (Shorrocks 1997), and B applied to coarse-textured soils is leached under excessive moisture (Rashid et al. 2007).

6.3 Boron cycling in rice-based agroecosystems

In soil, B exists in three compartments—soil solution, clay minerals, and organic matter. Applied or inherent B reacts in various ways in the soil including precipitation with calcium carbonates and sorption on clay or organic matter. Boron occurs naturally in soil or ground water or is added to soil from fertilizers, mining, or irrigation water (Nable et al. 1997); moreover, in rice-based systems, B has different fates depending on the prevailing climatic conditions. Boron in soil solution is readily available and is easily taken up by plants; however, this fraction is < 3% of the total B in soil (Tsadilas et al. 1994). Boron is mainly taken up by plant roots through mass flow especially when B concentrations in the soil solution are more than adequate.

Applied B may undergo rapid leaching from the soil (Parker and Gardner 1982), or it moves from above the Ap horizon (plowed or disturbed soil) to the BA horizon (dominant properties of one horizon but some properties of other horizons) and Bt1 horizon (showing clay accumulation) (Pinyerd et al. 1984). Under such conditions, some fertilizer B from the subsurface horizons is retrieved by deep roots, which leads to a long-term residual effect (Yang et al. 2000). The other fate of applied B in rice-based cropping systems is the removal of B through crop harvesting either as grains or stubble (Wang et al. 1997). According to Wang et al. (1999), the removal of 40% applied B by crops in intensively cultivated rice-based systems diminishes the residual value of fertilizer B. Therefore, in an oilseed rape–rice system in southeast China, basal application of $1.1\text{--}1.65 \text{ kg B ha}^{-1}$ to soil every 3 years is recommended (Yang et al. 2000). However, in multilocation, multiyear rice–wheat rotation field trials in B-deficient calcareous soils of Pakistan, Rashid et al. (2007) observed a beneficial residual effect on three successive crops from a moderate rate of soil-applied B (1.00 kg ha^{-1}) to rice (Table 7).

The management of crop (especially rice) residues by recycling these and manures into the soil becomes a primary factor for controlling the long-term B balance in the soil. Organic matter turnover is vital for B cycling in soils and is closely associated with B availability (Swarup 1991).

Table 6 Residual effect of soil-applied B in various rice production systems on rice productivity

B source	Boron application (crop/rate)	Production system	Soil texture	Soil pH	Increase in grain (paddy) yield over control (%)	Country	Reference
B fertilizer	Rape @ $1.1\text{--}3.3 \text{ kg B ha}^{-1}$	Wetland rice	Silty	6.5	0.81–3.23	China	Yang et al. (2000)
B fertilizer	Rape @ $1.1\text{--}3.3 \text{ kg B ha}^{-1}$	Wetland rice	Clay	5.1	2.61–3.48	China	Yang et al. (2000)
B fertilizer	Rape @ $1.1\text{--}3.3 \text{ kg B ha}^{-1}$	Wetland rice	Sandy	5.1	0.38–4.25	China	Yang et al. (2000)
B fertilizer	Rape @ $1.1\text{--}3.3 \text{ kg B ha}^{-1}$	Upland rice	Clay	6.4	1.24	China	Yang et al. (2000)
$\text{Na}_2\text{B}_4\text{O}_7 \cdot 5\text{H}_2\text{O}$	Soybean @ $1.12\text{--}8.96 \text{ kg B ha}^{-1}$	Direct seeding in aerobic culture	Silt loam	6.3	2.56	USA	Slaton et al. (2004)

Table 7 Crop responses and economics of soil-applied boron fertilizer to rice in Pakistan (*N* = number of field trials)

Rice cultivar	Rice-growing region	<i>N</i>	B applied (kg ha ⁻¹)	Control yield (t ha ⁻¹)	Yield increase (%)	Value:cost ratio ¹
Super Basmati	Punjab	24	1	3.04	21	36:1
Basmati-385	Punjab	8	1	3.74	21	45:1
KS-282	Punjab	3	1	4.82	14	26:1
IR-6	Sindh	10	1	4.34	30	25:1

Source: Anonymous (1998) and Rashid et al. (2007)

¹ Based on local prices of commercial-grade borax, boric acid, and crop produce

6.4 Boron use recommendations

For cost-effective and safe use of fertilizer B in rice-based cropping systems, consideration should be given to (i) the uniform field broadcasting of B fertilizer by premixing with major nutrient fertilizers or with well-pulverized soil and (ii) presowing application to soil, along with other basal fertilizers. Based on periodic soil test results, B fertilizer is generally applied to the main cash crop in the rotation, i.e., to rice in the rice–wheat system. Sandy soils may require annual B application, while less permeable finer-textured soils require one application every 2–3 years (Yang et al. 2000; Rashid 2006). Boron can also be applied to crops using alternative methods including foliar application and the dipping of rice seedlings in B solution. However, the B use efficiency of these methods varies with the age of the crop, rate of B used, and soil and environmental factors.

6.5 Boron toxicity hazard in rice?

Boron toxicity is a common problem in arid and semiarid regions of the world where B concentrations in the soil or irrigation water are high (Nable et al. 1997). Due to an excessive rate of B fertilizer, B toxicity symptoms can appear in crop plants grown on alkaline soils (Havlin et al. 1999; Singh et al. 1990). High B concentrations in the soil, usually from 1 to 5 mM, inhibit root and shoot growth (Reid et al. 2004). Necrosis, chlorosis, brownish leaf tips, reduced root and shoot elongation, and dark brown elliptical spots on leaves are prominent symptoms of B toxicity (Fig. 1). Moreover, excessive B inhibits starch synthesis or forms B-carbohydrate complexes resulting in retarded grain formation (Das 2014). Boron spontaneously interacts with diol groups in the *cis* position; therefore, metabolic reactions involving *cis*-diol compounds including RNA, NADP, and ATP are considered specific injury sites (Power and Woods 1997). Boron in high supply accumulates around the end of leaf veins, and the pattern of toxicity symptoms is related to the pattern of leaf venation. Therefore, uniform field distribution of small amounts of B

fertilizer must be ensured by mixing it with major nutrient fertilizers. In rice–wheat rotations on the calcareous soils of Pakistan, B fertilizer applied to rice crops (0.5–1.5 kg B ha⁻¹) had no toxic effect on the productivity of rice or wheat (Rashid, unpublished data). As repeated applications of the recommended dose of B fertilizer may become toxic, depending upon B rate and soil types, fields receiving B fertilizer must be monitored for their soil B status every 3–4 years (Rashid et al. 2007).

6.6 Constraints to boron fertilizer user

In Pakistan, available reports on B deficiency in rice are 40 years old (Chaudhry et al. 1976). However, the realization of widespread B deficiency and its adverse impact on rice productivity and grain quality is more recent. Despite highly cost-effective returns to investment in B fertilizer (improved productivity and grain quality), B fertilizer use in rice remains much lower than required. There are several constraints to B fertilizer use: (i) lack of farmer knowledge about the need for B fertilizers, (ii) lack of financial access to B fertilizers, (iii) nonavailability of B-fortified major nutrient fertilizer products, and (iv) difficulty in applying small quantities of B fertilizer, to achieve uniform field broadcast or for mixing it with major nutrient fertilizers, or for preparing correct spray solutions (Rashid 2006; Rashid et al. 2017).

7 Improving boron utilization and partitioning

Since B is phloem immobile in most plant species, a continuous supply of B is needed during all stages of plant growth (Brown and Shelp 1997); phloem recycling of B does not happen in rice. Boron use efficiency depends on its uptake, utilization, or retranslocation by the plant (Wang et al. 2007). The following genetic manipulation approaches could be employed to improve B use efficiency in rice.

7.1 Conventional breeding

Developing B-efficient cultivars for the widespread B-deficient soils is important for improving rice productivity. Genetic variation in B acquisition and efficiency in biomass production has been manipulated in many crop species to manage B deficiency (Rerkasem and Jamjod 1997). Enhanced B transport into wheat ears has been identified as a mechanism for enhancing B efficiency (NaChiangmai et al. 2004). Conventional breeding may be an important option for developing cultivars with the ability to cope with short-term B deficiency. Polyols have been identified as transporting molecules and are helpful for alleviating short-term B deficiency due to their ability to retranslocate B within the plant. Polyol synthesis is, therefore, important for the selection or genetic manipulation of plants with an improved ability to retranslocate internal B, resulting in a cultivar with a high B concentration (Brown and Shelp 1997).

7.2 Molecular and biotechnological approaches

Molecular approaches are important for understanding B translocation and movement through various channels and transporters and its absorption. For this purpose, different transgenic lines with identical morphological and developmental characteristics and variable expression of water channel proteins can be employed (Huang et al. 2005). As B is highly permeable in the lipid bilayer, its estimated lipid permeability coefficient is $8 \times 10^{-6} \text{ cm s}^{-1}$ (Raven 1980). Given its high membrane permeability, B uptake by passive diffusion across the lipid bilayer will only be significant for a high concentration gradient (high B supply), but under B-deficient conditions, it may not be possible (Tanaka and Fujiwara 2008). Under low B conditions, membrane proteins are needed to fulfill a plant's boric demand (Tanaka and Fujiwara 2008). Gene transfer, using an efficient molecular approach, could assist in the transfer of the B-efficient trait in the classical aromatic Basmati cultivar (Basmati-370) to the widespread newer rice varieties. However, first, the genetic basis for greater B efficiency in Basmati cultivars needs to be determined. Different transporters for efficient uptake of B by plant roots, xylem loading, and distribution have been reported (Fig. 2); these transporters have a potential role in acquisition and utilization of B. Genes encoding these transporters regulated the response to B availability in the environment to ensure tissue B homeostasis (Miwa and Fujiwara 2010).

7.3 Agronomic approaches

Various agronomic approaches are useful for improving the B status of plants. While the effect of tillage on B in different rice-based production systems has not been reported, it is

known that organic matter decomposition and soil aeration help in the release of adsorbed B (Mahler et al. 1985). Crop rotations are advocated for improving different soil properties, such as organic matter content, and better cation exchange capacity which influences the availability of B (Mahler et al. 1985). Organic manures offer plant nutrients including micronutrients by altering the biological, chemical, and physical properties of soils (Eghball et al. 2004). Manures affect B accumulation by adding organic matter (OM) to the soil (Marschner 1995). Moreover, the addition of farmyard manure (FYM) to soil improves the availability of native and added B to plants (Sharma et al. 1999), increases B retention in soil, and reduces leaching losses (Sharma et al. 2006). The application of B-coated urea helps to improve plant growth by providing B in a plant-available form, and enhance nitrogen use efficiency (Goodwin 2017; Shivay et al. 2017) because boron-coated urea fertilizer also improves the uptake of nitrogen in cereals (Singh 2013). Urea-coated B fertilizers improved plant growth due to better retention and uptake of both nitrogen and B; moreover, boric acid or other boron-containing compounds act as urease inhibitors that reduces urea volatilization losses as ammonium (Goodwin 2017). In addition, the development of boron-coated urea fertilizers is a promising option for farmers to apply B to the soil with the N fertilizer with minimal additional investment (Shivay et al. 2017). The application of micronutrients (e.g., boron), with organic or poultry manure, substantially improves soil fertility status and enhances the efficiency of applied nutrients (Bhuiyan 1994). The nutrient status in straw and grains can also be improved with poultry manure and B fertilizer application. Cumulative application of B to rice crops, either through soil, foliar, or seed treatments, is a reliable method for improving growth and development and enhancing B content in grains (Khan et al. 2006). Using powder colemanite [2 and 3 kg B ha^{-1}] as a B source rather than granular colemanite improved growth and yield of rice under flooded conditions (calcareous soil) due to a better supply of B to the rice crop (Saleem et al. 2013).

8 Conclusions and future research thrusts

Rice, a major staple cereal around the world, is suffering yield and quality losses due to soil B deficiency, particularly in rice-growing areas of Asia. Although new varieties with higher yield potentials have been developed and micronutrient management has improved, B deficiency in rice-based systems is still a major threat to crop productivity. Soil B deficiency reduces rice productivity through increased panicle sterility, fewer productive tillers, shriveled grains, fewer chloroplasts, and lower net assimilate rates along with impaired grain cooking quality. Boron deficiency may occur due to several factors including soil conditions, e.g., high pH, low organic

matter content, and water deficit. Furthermore, several environmental factors such as high temperature, light, and air humidity may cause B deficiency even in the presence of significant quantities of B.

The application of B (fertilizers) in different rice-based systems helps to increase crop productivity by reducing yield losses, enhancing milling return, and improving cooking quality. Furthermore, B fertilization is highly cost-effective, so rice growers are encouraged to include B in their fertilizer programs. Future research on rice-based systems should focus on breeding approaches, including marker-assisted selection and wide hybridization (incorporation of desirable genes), and biotechnological strategies, such as next-generation DNA and RNA sequencing, and genetic transformations to develop rice genotypes with improved B contents and abilities to acquire B from the soil. Moreover, different B application strategies—seed priming and foliar and/or soil application—should be included to improve the performance of rice, particularly when grown under aerobic conditions. Comprehensive and long-term research is needed on the accumulation and distribution of B using different resources; moreover, the application of B-enriched fertilizer with primary nutrients in rice crops should be studied to ascertain their interactions and availability under flooded and aerobic conditions. The role of B in controlling diseases and insects in field crops, particularly rice, should also be investigated. GIS-based mapping can be used to explore B-deficient rice zones/regions to determine the most suitable source of B fertilizer and application method to enhance B efficiency. Moreover, close consideration should be given to the consumption of micronutrients in humans with respect to their health rather than just their role in plants.

Funding information Financial support provided by the Higher Education Commission of Pakistan for the study is highly acknowledged.

References

- Abbas M, Zahida TM, Uddin R, Sajjid I, Akhlaq A, Moheyuddin K, Salahuddin J, Mari AH, Panhwar RN (2013) Effect of zinc and boron fertilizers application on some physicochemical attributes of five rice varieties grown in agro-ecosystem of Sindh, Pakistan. *American-Eurasian J Agric Environ Sci* 13:433–439
- Ahmad R, Irshad M (2011) Effect of boron application time on yield of wheat, rice and cotton crop in Pakistan. *Soil Environ* 30:50–57
- Ahmad W, Niaz A, Kanwal S, Rahmatullah, Rasheed MK (2009) Role of boron in plant growth: a review. *J Agric Res* 47:1122–1134
- Ahmad W, Zia MH, Malhi SS, Niaz A, Saifullah (2012) Boron deficiency in soils and crops: a review. In: Goyal A (Ed.) *Crop plant*. InTech, London, UK, pp 77–114
- Anonymous (1998) *Micronutrients in agriculture: Pakistani perspective*. Islamabad (Pakistan): National Fertilizer Development Center, Islamabad
- Aslam M, Mahmood IH, Qureshi RH, Nawaz S, Akhtar J (2002) Salinity tolerance of rice as affected by boron nutrition. *Pak J Soil Sci* 21: 110–118
- Bassil E, Hu H, Brown PH (2004) Use of phenylboronic acids to investigate boron function in plants. Possible role of boron in transvacuolar cytoplasmic strands and cell-to-wall adhesion. *Plant Physiol* 136:3383–3395
- Bell RW (1997) Diagnosis and prediction of boron deficiency for plant production. *Plant Soil* 193:149–168
- Bell RW, Dell B (2008) *Micronutrients for sustainable food, feed, fiber and bioenergy production*, 1st edn. IFA, Paris
- Bergmann W (1992) *Nutritional disorders of plants*. Gustav Fisher Verlag, Stuttgart
- Bhatnagar RS, Attri SC, Mathur GS, Chaudhary RS (1979) Boron adsorption equilibrium in soils. *Ann Arid Zone* 18:86–95
- Bhuiyan NJ (1994) Crop production trends and need of sustainability in agriculture. Paper presented at the workshop on 'Integrated Nutrient Management for Sustainable Agriculture, held at Soil Resource Development Institute, Dhaka, Bangladesh June 26–28
- Bingham FT (1973) Boron in cultivated soils and irrigation waters. *Adv Chem* 123:130–138
- Blaser-Grill J, Knoppik D, Amberger A, Goldbach H (1989) Influence of boron on the membrane potential in *Elodea densa* and *Helianthus annuus* roots and H⁺ extrusion of suspension cultured *Daucus carota* cells. *Plant Physiol* 90:280–284
- Blevins DG, Lukaszewski KM (1998) Boron in plant structure and function. *Annu Rev Plant Physiol Plant Mol Biol* 49:481–500
- Bolaños L, Brevin NJ, Bonilla I (1996) Effects of boron on Rhizobium-legume cell-surface interactions and nodule development. *Plant Physiol* 110:1249–1256
- Bolaños L, Lukaszewski K, Bonilla I, Blevins D (2004) Why boron? *Plant Physiol Biochem* 42:907–912
- Bonilla I, El-Hamdaoui A, Bolaños L (2004) Boron and calcium increase *Pisum sativum* seed germination and seedling development under salt stress. *Plant Soil* 267:97–107
- Bouman BAM, Tuong TP (2001) Field water management to save water and increase its productivity in irrigated rice. *Agric Water Manag* 49: 11–30
- Bouman BAM, Peng S, Castañeda AR, Visperas RM (2005) Yield and water use of irrigated tropical aerobic rice systems. *Agric Water Manag* 74:87–105
- Bowen JE (1972) Effect of environmental factors on water utilisation and boron accumulation and translocation in sugarcane. *Plant Cell Physiol* 13:703–714
- Brenchley WE, Thornton HG (1925) The relation between the development, structure and functioning of the nodules on *Vicia uha*, as influenced by the presence or absence of boron in the nutrient medium. *Proc R Soc Lond B Biol Sci* 498:373–398
- Brown PH, Shelp BJ (1997) Boron mobility in plants. *Plant Soil* 193:85–101
- Brown PH, Bellaloui N, Wimmer MA, Bassil ES, Ruiz J, Hu H, Pfeiffer H, Dannel F, Römhelt V (2002) Boron in plant biology. *Plant Biol* 4:211–229
- Butterwick L, Oude ND, Raymond K (1989) Safety assessment of boron in aquatic and terrestrial environments. *Ecotoxicol Environ Saf* 17: 339–371
- Cakmak I, Römhelt V (1997) Boron deficiency-induced impairments of cellular functions in plants. *Plant Soil* 193:71–83
- Chapman HD, Vaselew AP (1955) Boron deficiency and excess. *Calif Citogr* 40:455–457
- Chatterjee C, Sinha P, Agarwala SC (1990) Interactive effect of boron and phosphorus on growth and metabolism of maize grown in refined sand. *Can J Plant Sc* 70:455–460
- Chaudhry FM, Latif A, Sharif M, Rashid A, Alam SM (1976) Response of the rice varieties to field application of micronutrient fertilizers. *Pakistan J Sci Indus Res* 19:134–139
- Chen X, Schauder S, Potier N, Van Dorsselaer A, Pelczar I, Bassler B, Hughson FM (2002) Structural identification of a bacterial quorum-sensing signal containing boron. *Nature* 415:545–549
- Coulthurst SJ, Whitehead NA, Welch M, Salmond GPC (2002) Can boron get bacteria talking? *Trends Biochem Sci* 27:217–219

- Darvill A, McNeil M, Albersheim P, Delmer DP (1980) The primary cell wall of flowering plants. In: Tolbert NE, Corn PK, Eric E, Stumph PK, Conn EE (eds) The biochemistry of plants. A comprehensive treatise. Academic, New York, pp 91–161
- Das SK (2014) Role of micronutrient in rice cultivation and management strategy in organic agriculture—a reappraisal. *Agric Sci* 5:765–769
- De Datta SK (1981) Principles and practices of rice production. Wiley, New York
- Dell B, Huang L (1997) Physiological response of plants to low boron. *Plant Soil* 193:103–120
- Depar N, Rajpar I, Memon MY, Imtiaz M, Zia-ul-Hassan (2011) Mineral nutrient densities in some domestic and exotic rice genotypes. *Pak J Agric Agril Eng Vet Sci* 27:134–142
- Diana G (2006) Boron in the soil, from deficit to toxicity. *Informatore Agrario* 62:54–58
- Diaz FJ, Grattan SR (2009) Performance of tall wheatgrass (*Thinopyrum ponticum*, cv. ‘Jose’) irrigated with saline-high boron drainage water: implications on ruminant mineral nutrition. *Agric Ecosyst Environ* 131:128–136
- Dixit D, Srivastava NK, Sharma S (2002) Boron deficiency induced changes in translocation of $^{14}\text{CO}_2$ -photosynthate into primary metabolites in relation to essential oil and curcumin accumulation in turmeric (*Curcuma longa* L.). *Photosynthetica* 40:109–113
- Dordas C, Brown PH (2000) Permeability of boric acid across lipid bilayers and factors affecting it. *J Membr Biol* 175:95–105
- Dugger WM (1983) Boron in plant metabolism. In: Laëuchli A, Bielecki RL (eds) Inorganic plant nutrition. Encyclopedia of plant physiology. Springer, Berlin, pp 626–650
- Dunn D, Stevens G, Kending A (2005) Boron fertilization of rice with soil and foliar applications. *Online Crop Manag.* <https://doi.org/10.1094/CM-2005-0210-01-RS>
- Eck P, Campbell FJ (1962) Effect of high calcium application on boron tolerance of carnation, *Dianthus caryophyllus*. *Am Soc Hort Sci Proc* 81:510–517
- Eghball B, Ginting D, Gilley JE (2004) Residual effects of manure and compost applications on corn production and soil properties. *Agron J* 96:442–447
- Elrashidi MA, O'Connor GA (1982) Boron sorption and desorption in soils. *Soil Sci Soc Am J* 46:27–31
- El-Shintinawy F (2000) Structural and functional damage caused by boron deficiency in sunflower leaves. *Photosynthetica* 36:565–573
- Fageria NK, Baligar VC (2003) Methodology for evaluation of lowland rice genotypes for nitrogen use efficiency. *J Plant Nutr* 26:1315–1333
- FAO (2016) The state of food and agriculture, climate change, agriculture and food security. FAO, Rome
- Farooq M, Basra SMA, Wahid A (2006a) Priming of field-sown rice seed enhances germination, seedling establishment, allometry and yield. *Plant Growth Regul* 49:285–294
- Farooq M, Basra SMA, Tabassum R, Afzal I (2006b) Enhancing the performance of direct seeded fine rice by seed priming. *Plant Prod Sci* 9:446–456
- Farooq M, Basra SMA, Khalid M, Tabassum R, Mehmood T (2006c) Nutrient homeostasis, reserves metabolism and seedling vigor as affected by seed priming in coarse rice. *Can J Bot* 84:1196–1202
- Farooq M, Basra SMA, Khan MB (2007a) Seed priming improves growth of nursery seedlings and yield of transplanted rice. *Arch Agron Soil Sci* 53:311–322
- Farooq M, Basra SMA, Ahmad N (2007b) Improving the performance of transplanted rice by seed priming. *Plant Growth Regul* 51:129–137
- Farooq M, Rehman A, Aziz T, Habib M (2011) Boron nutrimpriming improves the germination and early seedling growth of rice (*Oryza sativa* L.). *J Plant Nutr* 34:1507–1515. <https://doi.org/10.1080/01904167.2011.585207>
- Fleischer A, O'Neill MA, Ehwald R (1999) The pore size of non-graminaceous plant cell walls is rapidly decreased by borate ester cross-linking of the pectic polysaccharide rhamnogalacturonan II. *Plant Physiol* 121:829–838
- Furlani AMC, Carvalho CP, de Freitas JP, Verdial MF (2003) Wheat cultivar tolerance to boron deficiency and toxicity in nutrient solution. *Sci Agric* 60:359–370. <https://doi.org/10.1590/S0103-90162003000200022>
- Gao S, Tanji KK, Scardaci SC, Chow AT (2002) Comparison of redox indicators in a paddy soil during rice growing season. *Soil Sci Soc Am J* 66:805–817
- Gao XP, Zou CQ, Fan XY, Zhang FS, Hoffland E (2006) From flooded to aerobic conditions in rice cultivation: consequences for zinc uptake. *Plant Soil* 280:41–47. <https://doi.org/10.1007/s11104-004-7652-0>
- Gao X, Hoffland E, Stomph TJ, Grant CA, Zou C, Zhang F (2012) Improving zinc bioavailability in transition from flooded to aerobic rice: a review. *Agron Sustain Dev* 32:465–478. <https://doi.org/10.1007/s13593-011-0053-x>
- Goldbach HE, Wimmer MA (2007) Boron in plants and animals: is there a role beyond cell-wall structure? *J Plant Nutr Soil Sci* 170:39–48. <https://doi.org/10.1002/jpln.200625161>
- Goldbach HE, Yu Q, Wingender R, Schulz M, Wimmer M, Findeklee P, Baluska F (2001) Rapid response reactions of roots to boron deprivation. *J Plant Nutr Soil Sci* 164:173–181
- Goldbach H, Huang L, Wimmer M (2007) Boron functions in plants and animals: recent advances in boron research and open questions. In: Xu F, Goldbach HE, Brown PH, Bell RW, Fujiwara T, Hunt CD, Goldberg S, Shi L (eds) Advances in plant and animal boron nutrition. Springer, Dordrecht, pp 3–25
- Goldberg S (1997) Reactions of boron with soils. *Plant Soil* 193:35–48. <https://doi.org/10.1023/A:1004203723343>
- Goldberg S, Glaubig RA (1986) Boron adsorption on California soils. *Soil Sci Soc Am J* 50:1173–1176
- Goldberg S, Corwin DL, Shouse PJ, Suarez DL (2005) Prediction of boron adsorption by field samples of diverse textures. *Soil Sci Soc Am J* 69:1379–1388
- Goodwin M (2017) Urea fertilizers coated with plant available forms of boron. U.S. Patent Application 15/234:704
- Gowri S (2005) Physiological studies on aerobic rice (*Oryza sativa* L.). M.Sc. Thesis, Tamil Nadu Agriculture University, Coimbatore, India
- GRiSP (Global Rice Science Partnership) (2013) Rice almanac, 4th edn. International Rice Research Institute, Los Baños
- Gu B, Lowe LE (1990) Studies on the adsorption of boron on humic acid. *Can J Soil Sci* 70:305–311
- Günes A, Alpaslan M (2000) Boron uptake and toxicity in maize genotypes in relation to boron and phosphorus supply. *J Plant Nutr* 23: 541–550. <https://doi.org/10.1080/01904160009382038>
- Gupta UC (1968) Relationship of total and hot-water soluble boron, and fixation of added boron, to properties of Podzol soils. *Soil Sci Soc Am Proc* 32:45–48
- Gupta UC (1979) Boron nutrition of crops. *Adv Agron* 31:273–307
- Gupta UC (1993) Introduction. In: Gupta UC (ed) Boron and its role in crop production. CRC, Boca Raton, p 237
- Gupta PC, O'Toole JC (1986) Upland rice: a global perspective. International Rice Research Institute, Manila
- Gupta UC, Sterling JDE, Nass HG (1973) Influence of various rates of compost and nitrogen on the boron toxicity symptoms in barley and wheat. *Can J Plant Sci* 53:451–456
- Harris D, Tripathi RS, Joshi A (2002) On-farm seed priming to improve crop establishment and yield in dry direct-seeded rice. In: Pandey S, Mortimer M, Wade L, Tuong TP, Lopes K, Hardy B (eds) Direct seeding: research strategies and opportunities. International Research Institute, Manila, pp 231–240
- Havlin JL, Beaton JD, Tisdale SL, Nelson WL (1999) Soil fertility and fertilizers. Prentice-Hall, London
- Hellal FA, Taalab AS, Safaa AM (2009) Influence of nitrogen and boron nutrition on nutrient balance and sugar beet yield grown in calcareous soil. *Ozean J Appl Sci* 2:95–112

- Hou J, Evans LJ, Spiers GA (1994) Boron fractions in soils. *Commun Soil Sci Plant Anal* 25:1841–1853. <https://doi.org/10.1080/00103629409369157>
- Hu H, Brown PH (1997) Absorption of boron by plant roots. *Plant Soil* 193:49–58. <https://doi.org/10.1023/A:1004255707413>
- Hu H, Brown PH, Labavitch JM (1996) Species variability in boron requirement is correlated with cell wall pectin. *J Exp Bot* 47:227–232
- Huang J, Snapp SS (2009) Potassium and boron nutrition enhance fruit quality in Midwest fresh market tomatoes. *Commun Soil Sci Plant Anal* 40:1937–1952
- Huang L, Pant J, Dell B, Bell RW (2000) Effects of boron deficiency on anther development and floret fertility in wheat (*Triticum aestivum* L. cv. Wilgozne). *Ann Bot* 85:493–500
- Huang L, Bell RW, Dell B (2001) Boron supply into wheat (*Triticum aestivum* L., cv. Wilgozne) ears whilst still enclosed within leaf sheaths. *J Exp Bot* 52:1731–1738
- Huang L, Ye Z, Bell RW, Dell B (2005) Boron nutrition and chilling tolerance of warm climate crop species. *Ann Bot* 96:755–767
- Huettl PJV (1976) The pH dependent sorption of boron by soil organic matter. M.Sc. thesis, University of Wisconsin, Madison, Wisconsin, USA
- Hussain M, Khan MA, Khan MB, Farooq M, Farooq S (2012) Boron application improves growth, yield and net economic return of rice. *Rice Sci* 19:259–262. [https://doi.org/10.1016/S1672-6308\(12\)60049-3](https://doi.org/10.1016/S1672-6308(12)60049-3)
- Isirimah NO, Dickson AA, Igwe C (2003) Introductory soil chemistry and biology for agriculture and biotechnology. OSIA International Publishers Ltd., Port Harcourt
- Ismail AM (2003) Response of maize and sorghum to excess boron and salinity. *Biol Plantarum* 47:313–316
- Jame YW, Nickolaichuk W, Leyshon AJ, Campbell CA (1982) Boron concentration in the soil solution under irrigation. A theoretical analysis. *Can J Soil Sci* 62:461–470
- Jasmund K, Lindner B (1973) Experiments on the fixation of boron by clay minerals. *Proc Int Clay Conf* 1972:399–412
- Jin J, Martens DC, Zelazny LW (1987) Distribution and plant availability of soil; boron fractions. *Soil Sci Soc Am J* 51:1228–1231
- Jin JY, Martens DC, Zelazny LW (1988) Plant availability of applied and native boron in soils with diverse properties. *Plant Soil* 105:127–132. <https://doi.org/10.1007/BF02371150>
- Jones JB (2003) Plant mineral nutrition. In: *Agronomic handbook: management of crops, soils and their fertility*. CRC, Boca Raton, Boca Raton, FL, USA, p 325
- Jones JB Jr, Wolf B, Mills HA (1991) *Plant analysis handbook: a practical sampling, preparation, analysis and interpretation guide*. Micro-Macro Inc., Athens
- Jones WW, Embleton TW, Boswell SB, Steinacker ML, Lee BW, Barnhart EL (1963) Nitrogen control programme for oranges and high sulphate and/or high boron. *Calif Citrogr* 48:128–129
- Kastori R, Plesnicar M, Pankovic D, Sakac Z (1995) Photosynthesis, chlorophyll fluorescence and soluble carbohydrates in sunflower leaves as affected by boron deficiency. *J Plant Nutr* 18:1751–1763
- Katyal JC, Singh B (1992) Availability of boron in the soil and its uptake by rice as influenced by soil moisture regimes. *Oryza* 29:384–387
- Kausar MA, Tahir M, Hamid A (1990) Comparison of three methods for the estimation of soil available boron for maize. *Pak J Sci Ind Res* 33:221–224
- Keren R, Bingham FT (1985) Boron in water, soil and plants. *Adv Soil Sci* 1:229–276
- Keren R, Mezuman U (1981) Boron adsorption by clay minerals using a phenomenological equation. *Clay Clay Miner* 29:198–203
- Keren R, Talpaz H (1984) Boron adsorption by montmorillonite as affected by particle size. *Soil Sci Soc Am J* 48:555–559
- Keren R, Bingham FT, Rhoades JD (1985) Plant uptake of boron as affected by boron distribution between liquid and solid phases in soil. *Soil Sci Soc Am J* 49:297–302
- Khan R, Gurmani AH, Gurmani AR, Zia MS (2006) Effect of boron application on rice yield under wheat–rice system. *Int J Agric Biol* 8:805–808
- Khan RU, Gurmani AR, Khan MS, Jalal-Ud-Din, Gurmani AH (2011) Residual, direct and cumulative effect of boron application on wheat and rice yield under rice-wheat system. *Sar J Agric* 27:219–223
- Kobayashi M, Ohno K, Matoh T (1997) Boron nutrition of cultured tobacco BY-2 cells. II. Characterisation of the boron polysaccharide complex. *Plant Cell Physiol* 38:676–683. <https://doi.org/10.1093/oxfordjournals.pcp.a029220>
- Kohorn BD, Kobayashi M, Johansen S, Friedman HP, Fischer A, Byers N (2006) Wall-associated kinase 1 (WAK1) is crosslinked in endomembranes, and transport to the cell surface requires correct cell-wall synthesis. *J Cell Sci* 119:2282–2290
- Koohkan H, Maftoun M (2015) Effect of nitrogen on the alleviation of boron toxicity in rice (*Oryza sativa* L.). *J Plant Nutr* 38:1323–1335
- Kumar S, Arora BR, Hundal HS (1981) Potassium–boron synergism in the nutrition of rice (*Oryza sativa* L.). *J Indian Soc Soil Sci* 29:563–564
- Lambert DH, Cole HC, Baker DE (1980) The role of boron in plant response to mycorrhizal infection. *Plant Soil* 57:431–438
- Lehto L (1995) Boron retention in limed forest floor. *For Ecol Manag* 78: 11–20. [https://doi.org/10.1016/0378-1127\(95\)03599-7](https://doi.org/10.1016/0378-1127(95)03599-7)
- Liu Z (1996) Soil microelement in China. Jiangsu Science Technical Press, Nanjiang, pp 25–47
- Lordkaew S, Konsaeng S, Jongjaidee J, Dell B, Rerkasem B, Jamjod S (2013) Variation in responses to boron in rice. *Plant Soil* 363:287–295
- Lucas RE, Knezek BD (1972) Climatic and soil conditions promoting micronutrient deficiencies in plants. In: Mortvedt JJ et al (eds) *Micronutrients in agriculture*. Soil Science Society of America, Madison, pp 265–288
- Maclean JL, Dawe DC, Hardy B, Hettel CP (2002) *Rice almanac*, 3rd edn. CABI, Wallingford
- Mahler RL, Hammel JE, Harder RW (1985) The influence of crop rotation and tillage methods on the distribution of extractable boron in northern Idaho soils. *Soil Sci* 139
- Marschner H (1995) Mineral nutrition of higher plants. Academic, San Diego
- Masood S, Wimmer MA, Witzel K, Zörb C, Mühling KH (2012) Interactive effects of high boron and NaCl stresses on subcellular localization of chloride and boron in wheat leaves. *J Agron Crop Sci* 198:227–235
- Matoh T (1997) Boron in plant cell walls. *Plant Soil* 193:59–70. <https://doi.org/10.1023/A:1004207824251>
- Matoh T, Kobayashi M (1998) Boron and calcium, essential inorganic constituents of pectic polysaccharides in higher plant cell walls. *J Plant Res* 111:179–190
- Matoh T, Kawaguchi S, Kobayashi M (1996) Ubiquity of a borate-rhamnogalacturonan II complex in the cell walls of higher plants. *Plant Cell Physiol* 37:636–640
- Matoh T, Takasaki M, Takabe K, Kobayashi M (1998) Immunocytochemistry of rhamnogalacturonan II in cell walls of higher plants. *Plant Cell Physiol* 39:483–491
- Matsunaga T, Ishii T, Matsumoto S, Higuchi M, Darvill A, Albersheim P, O'Neill MA (2004) Occurrence of the primary cell wall polysaccharide rhamnogalacturonan II in pteridophytes, lycophytes, and bryophytes. Implications for the evolution of vascular plants. *Plant Physiol* 134:339–351
- Mattigod SV, Frampton JA, Lim CH (1985) Effect of ion-pair formation on boron adsorption by kaolinite. *Clay Clay Miner* 33:433–437
- Mezuman U, Keren R (1981) Boron adsorption by soils using a phenomenological adsorption equation. *Soil Sci Soc Am J* 45:722–726
- Middleton W, Jarvis BC, Booth A (1978) The boron requirement for root development in stem cuttings of *Phaseolus aureus* Roxb. *New Phytol* 81:287–298
- Miwa K, Fujiwara T (2010) Boron transport in plants: co-ordinated regulation of transporters. *Ann Bot* 105:1103–1108

- Mortvedt JJ (1994) Boron diet essential for crops. Farm Chemicals, pp 2
- Nable RO, Banuelos GS, Paull JG (1997) Boron toxicity. *Plant Soil* 193: 181–198
- Nachiangmai D, Dell B, Bell RW, Huang L, Rerkasem B (2004) Enhanced boron transport into the ear of wheat as a mechanism for boron efficiency. *Plant Soil* 264:141–147
- Nakagawa Y, Hanaoka H, Kobayashi M, Miyoshi K, Miwa K, Fujiwara T (2007) Cell-type specificity of the expression of OsBOR1, a rice efflux boron transporter gene, is regulated in response to boron availability for efficient boron uptake and xylem loading. *Plant Cell* 19:2624–2635. <https://doi.org/10.1105/tpc.106.049015>
- Niaz A, Ranjha AM, Rahmatullah AH, Waqas M (2007) Boron status of soils as affected by different soil characteristics—pH, CaCO₃, organic matter and clay contents. *Pak J Agric Sci* 44:428–435
- Nicholaichuk W, Leyshon AJ, Jame YW, Campbell CA (1988) Boron and salinity survey of irrigation projects and the boron adsorption characteristics of some Saskatchewan soils. *Can J Soil Sci* 68:77–90
- Nieuwenhuis J, Bouman BAM, Castaneda A (2000) Crop–water responses of aerobically grown rice, preliminary results of pot experiments. In: Bouman BAM, Hengsdijk H, Hardy B, Bindraban PS, Tuong TP, Ladha JK (eds) Water wise rice production. Proceedings of a thematic workshop on water-wise rice production. 8–11 April 2002. IRRI Headquarters in Los Banos, Philippines, pp 177–186
- O'Neill MA, Ishii T, Albersheim P, Darvill AG (2004) Rhamnogalacturonan II: structure and function of a borate cross-linked cell wall pectic polysaccharide. *Annu Rev Plant Biol* 55: 109–139. <https://doi.org/10.1146/annurev.arplant.55.031903.141750>
- Obermeyer G, Kriechbaumer R, Strasser D, Maschessning A, Bentrup FW (1996) Boric acid stimulates the plasma membrane H⁺-ATPase of ungerminated lily pollen grains. *Physiol Plant* 98:281–290
- Okazaki E, Chao TT (1968) Boron adsorption and desorption by some Hawaiian soils. *Soil Sci* 105:255–259
- Pandey DK, Pandey N (2008) Screening of wheat genotypes for their susceptibility to boron deficiency. *Res Environ Life Sci* 1:37–42
- Pandey S, Velasco LE (1999) Economics of alternative rice establishment methods in Asia: a strategic analysis. Discussion Paper, Social Sciences Division Discussion Paper, International Rice Research Institute, Los Baños, Philippines
- Parker DR, Gardner EH (1982) Factors affecting the mobility and plant availability of boron in some western Oregon soils. *Soil Sci Soc Am J* 46:573–578
- Parks WL, White JL (1952) Boron retention by clays and humus systems saturated with various cations. *Soil Sci Soc Am Proc* 16:298–300
- Patrick JW, Wareing PF (1973) Auxin-promoted transport of metabolites in stems of *Phaseolus vulgaris* L. *J Exp Bot* 24:1158–1167
- Peterson LA, Newman RC (1976) Influence of soil pH on the availability of added boron. *Soil Sci Soc Am J* 40:280–282
- Pinyerd CA, Odom JW, Long FL, Dane JH (1984) Boron movement in a Norfolk loamy sand. *Soil Sci* 137:428–433
- Ponnamperuma FN, Yuan WL (1966) Toxicity of boron to rice. *Nature* 211:780
- Power PP, Woods WG (1997) The chemistry of boron and its speciation in plants. *Plant Soil* 193:1–13
- Prasad R (2011) Aerobic rice systems. *Adv Agron* 111:207–247. <https://doi.org/10.1016/B978-0-12-387689-8.00003-5>
- Rao PR, Subrahmanyam D, Sailaja B, Singh RP, Ravichandran V, Rao GS, Swain P, Sharma SG, Saha S, Nadarajan S, Reddy PJ (2013) Influence of boron on spikelet fertility under varied soil conditions in rice genotypes. *J Plant Nutr* 36:390–400
- Rashid A (2006) Boron deficiency in soils and crops of Pakistan: diagnosis and management. Pakistan Agriculture Research Council, Islamabad 34 pp
- Rashid A, Rafique E, Bughio N (1994) Diagnosing boron deficiency in rapeseed and mustard by plant analysis and soil testing. *Commun Soil Sci Plant Anal* 25:2883–2897
- Rashid A, Rafique E, Bughio N (1997) Micronutrient deficiencies in calcareous soils of Pakistan. III. Boron nutrition of sorghum. *Commun Soil Sci Plant Anal* 28:441–454
- Rashid A, Muhammad S, Rafique E (2000) Genotypic variation in rice susceptibility to boron deficiency. *Int Rice Res Notes* 25(3):29–30
- Rashid A, Muhammad S, Rafique E (2002a) Genotypic variation in boron uptake and utilization by rice and wheat. In: Goldbach HE, Rerkasem B, Wimmer MA, Brown PH, Thellier M, Bell RW (eds) Boron in plant and animal nutrition. Kluwer Academic, New York, pp 305–310
- Rashid A, Rafique E, Muhammed S, Bughio N (2002b) Boron deficiency in rainfed alkaline soils of Pakistan: incidence and genotypic variation in rapeseed-mustard. In: Goldbach HE, Rerkasem B, Wimmer MA, Brown PH, Thellier M, Bell RW (eds) Boron in plant and animal nutrition. Kluwer Academic/Plenum, New York, pp 363–370
- Rashid A, Rafique E, Ryan J (2002c) Establishment and management of boron deficiency in field crops in Pakistan: a country report. In: Goldbach HE, Rerkasem B, Wimmer MA, Brown PH, Thellier M, Bell RW (eds) Boron in plant and animal nutrition. Kluwer Academic/Plenum, New York, pp 339–348
- Rashid A, Yasin M, Ashraf M (2004) Boron deficiency in calcareous soil reduces rice yield and impairs grain quality. *Inter Rice Res Notes* 29: 58–60
- Rashid A, Yasin M, Ali MA, Ahmad Z, Ullah R (2007) An alarming boron deficiency in calcareous rice soils of Pakistan: boron use improves yield and cooking quality. In: Xu F (ed) Advances in plant and animal boron nutrition. Proc 3rd international symposium on all aspects of plant and animal boron nutrition, Wuhan, China, 9–13 Sep 2005. Springer, Dordrecht, pp 103–116
- Rashid A, Rafique E, Bhatti AU, Ryan J, Bughio N, Yau SK (2011) Boron deficiency in rainfed wheat in Pakistan: incidence, spatial variability, and management strategies. *J Plant Nutr* 34:600–613. <https://doi.org/10.1080/01904167.2011.538286>
- Rashid A, Zia MH, Ahmad W (2017) Micronutrient fertilizer use in Pakistan and 4R nutrient stewardship. Pakistan Agricultural Research Council and National Fertilizer Development Center, Islamabad 223 pp
- Raven JA (1980) Short- and long-distance transport of boric acid in plants. *New Phytol* 84:231–249
- Rawson HM (1996) Parameters likely to be associated with sterility. In: Rawson HM, Subedi KD (eds) Sterility in wheat in subtropical Asia: extent, causes and solutions. Proceedings of a workshop held from 18–21 September 1995, Lumle Agricultural Research Centre, Pokhara, Nepal. ACIAR Proceeding No. 72, pp 13–31
- Rehman A, Farooq M (2013) Boron application through seed coating improves the water relations, panicle fertility, kernel yield, and biofortification of fine grain aromatic rice. *Acta Physiol Plant* 35: 411–418
- Rehman A, Farooq M, Nawaz A, Iqbal S, Rehman A (2012a) Optimizing the boron seed coating treatments for improving the germination and early seedling growth of fine grain rice. *Int J Agric Biol* 14:453–456
- Rehman A, Farooq M, Cheema ZA, Wahid A (2012b) Seed priming with boron improves growth and yield of fine grain aromatic rice. *Plant Growth Regul* 68:189–201
- Rehman A, Farooq M, Cheema ZA, Wahid A (2013) Role of boron in leaf elongation and tillering dynamics in fine-grain aromatic rice. *J Plant Nutr* 36:42–54. <https://doi.org/10.1080/01904167.2012.733048>
- Rehman A, Farooq M, Nawaz A, Ahmad R (2014a) Influence of boron nutrition on the rice productivity, kernel quality and biofortification in different production systems. *Field Crops Res* 169:123–131
- Rehman A, Farooq M, Cheema ZA, Nawaz A, Wahid A (2014b) Foliage applied boron improves the panicle fertility, yield and biofortification of fine grain aromatic rice. *J Soil Sci Plant Nutr* 14:723–733

- Rehman A, Farooq M, Nawaz A, Rehman A, Iqbal S (2015) Soil application of boron improves the tillering, leaf elongation, panicle fertility, yield and its grain enrichment in fine-grain aromatic rice. *J Plant Nutr* 38:338–354
- Rehman A, Farooq M, Nawaz A, Ahmad R (2016) Improving the performance of short duration basmati rice in water-saving production systems by boron nutrition. *Ann Appl Biol* 168:19–28
- Reid RJ, Hayes JE, Post A, Stangoulis JCR, Graham RD (2004) A critical analysis of the causes of boron toxicity in plants. *Plant Cell Environ* 27:1405–1414
- Renkou X, Zhao A, Li Q, Kong X, Ji G (2003) Acidity regime of the Red Soils in a subtropical region of southern China under field conditions. *Geoderma* 115:75–84
- Rerkasem B, Jamjod S (1997) Genotypic variation in crop response to low boron and implications for plant breeding. *Plant Soil* 193:169–180
- Rerkasem B, Jamjod S (2004) Boron deficiency in wheat: a review. *Field Crop Res* 89:173–186
- Rerkasem B, Bell RW, Lordkaew S, Loneragan JF (1997) Relationship of seed boron concentration to germination and growth of soybean (*Glycine max* L. Merr.). *Nut Cycl Agroecosyst* 48:217–223
- Reuhs BL, Glenn J, Stephens SB, Kim JS, Christie DB, Glushka JG, Zablackis E, Albersheim P, Darvill AG, O'Neill MA (2004) L-galactose replaces L-fucose in the pectic polysaccharide rhamnogalacturonan II synthesized by the L-fucose-deficient murl Arabidopsis mutant. *Planta* 219:147–157
- Reuter DJ, Edwards DG, Wilhelm NS (1997) Temperate and tropical crops. In: Reuter DJ, Robinson JB (eds) *Plant analysis: an interpretation manual*, 2nd edn. CSIRO, Collingwood, pp 81–284
- Robertson GA, Loughman BC (1974) Modification of phosphate transport in *Vicia faba* by boron deficiency, growth regulators, and metabolic inhibitors. In: Zimmermann M, Dainty J (eds) *Membrane transport in plants*. Springer, New York, pp 444–449
- Roth-Bejerano N, Itai C (1981) Effect of boron on stomatal opening in epidermis strips of *Commelina communis*. *Physiol Plant* 52:302–304
- Ryden P, Sugimoto-Shirasu K, Smith AC, Findlay K, Reiter WD, McCann MC (2003) Tensile properties of Arabidopsis cell walls depend on both a xyloglucan cross-linked microfibrillar network and rhamnogalacturonan II-borate complexes. *Plant Physiol* 132:1033–1040
- Sahrawat KL (2005) Fertility and organic matter in submerged rice soils. *Curr Sci* 88:735–739
- Saleem M, Khanif YM, Ishak F, Samsuri AW (2009) Dissolution kinetics of boron fertilizers, boron release in soil and effect on rice. *Proc. 4th Int. Boron Symp.* 15–17 October, Eskisehir-Turkey, pp 467–471
- Saleem M, Khanif YM, Ishak F, Samsuri AW, Hafeez B (2011a) Importance of boron for agriculture productivity: a review. *Inter Res J Agric Sci Soil Sci* 1:293–300
- Saleem M, Khanif YM, Ishak YMF, Samsuri AW (2011b) Solubility and leaching of boron from borax and colemanite in flooded acidic soils. *Commun Soil Sci Plant Anal* 42:293–300
- Saleem M, Khanif YM, Fauziah CI, Samsuri AW, Hafeez B (2013) Efficacy of crushed ore colemanite as boron fertilizer for rice grown under calcareous soil conditions. *Pak J Agric Sci* 50:37–42
- Samet H, Cikili Y, Dursun S (2015) The role of potassium in alleviating boron toxicity and combined effects on nutrient contents in pepper (*Capsicum annuum* L.). *Bulgarian J Agric Sci* 21:64–70
- Sarwar N, Ali H, Irfan M, Akhter MT, Ali MT (2016) Boron nutrition under intermittent flooding and drying condition seems sustainable nutrient management technique in rice. *Cercetari Agronomice Moldova* 49:17–27
- Savithri P, Perumal R, Nagarajan R (1999) Soil and crop management technologies for enhancing rice production under micronutrient constraints. In: Balasubramanian V et al (eds) *Resource management in rice systems: nutrients*. Kluwer Academic, Dordrecht, pp 121–135
- Schalscha EB, Bingham FT, Galindo GG, Galvan HP (1973) Boron adsorption by volcanic ash soils in southern Chile. *Soil Sci Baltimore* 116:70–76
- Schon MK, Novacky A, Blevins DG (1990) Boron induces hyperpolarization of sunflower root cell membranes and increases membrane permeability to K^{+} . *Plant Physiol* 93:566–571
- Shafiq M, Maqsood T (2010) Response of rice to model based applied boron fertilizer. *J Agric Res* 48:303–314
- Shah JA, Memon MY, Aslam M, Nizamuddin D, Sial NA, Khan P (2011) Response of two rice varieties viz., khushboo-95 and mehak to different levels of boron. *Pak J Bot* 43:1021–1031
- Sharma PK, Nayyar VK (2004) Diagnosing micronutrient related constraints to productivity in Muktsar, Patiala, Hoshiarpur and Ludhiana Districts. Information technology for sustainable agriculture in Punjab (IT-SAP) UNDP-TIFAC sponsored project. Punjab Remote Sensing Centre. Ludhiana, Punjab, India, pp 1–18
- Sharma PN, Ramchandra T (1990) Water relations and photosynthesis in mustard plants subjected to boron deficiency. *Indian J Plant Physiol* 33:150–154
- Sharma KR, Srivastava PC, Ghosh D, Gangwar MS (1999) Effect of boron and farmyard manure application on growth, yields, and boron nutrition of sunflower. *J Plant Nutr* 22:633–640
- Sharma KR, Srivastava PC, Srivastava P, Singh VP (2006) Effect of farmyard manure application on boron adsorption-desorption characteristics of some soils. *Chemosphere* 65:769–777
- Shelp BJ (1988) Boron mobility and nutrition in broccoli (*Brassica oleracea* var. *italica*). *Ann Bot* 61:83–91
- Shelp BJ (1990) The influence of nutrition on partitioning in broccoli plants. *Commun Soil Sci Plant Anal* 21:49–60
- Shelp BJ (1993) Physiology and biochemistry of boron in plants. In: Gupta UC (ed) *Boron and its role in crop protection*. CRC, Boca Raton, pp 53–85
- Shivay YS, Prasad R, Pooniya V, Pal M, Bansal R (2017) Response of spring wheat to boron-coated urea and its effect on nitrogen use efficiency. *J Plant Nutr* 40:1920–1927
- Shorrocks VM (1997) The occurrence and correction of boron deficiency. *Plant Soil* 193:121–148. <https://doi.org/10.1023/A:1004216126069>
- Sillanpaa M (1972) Trace elements in soils and agriculture. Food and Agric. Org. UN, Rome
- Sillanpaa M (1982) Micronutrients and nutrient status of soils: a global study. *FAO Soils Bull. No. 48*. Food & Agriculture Organization of the United Nations, Rome 444 pp
- Singh MV (2013) Efficiency of boron fortified NPK fertilizer in correcting boron deficiency in some cereal and oilseeds crops in India. XVII International Plant Nutrition Colloquium 19–22 August & Boron Satellite Meeting 17–18 August, Istanbul, Turkey
- Singh BP, Singh A, Singh BN (1990) Response of rice (*Oryza sativa* L.) to zinc sulfate under mid-altitude conditions of Meghalaya. *Ind J Agric Sci* 60:70–71
- Slaton NA, Ross JR, DeLong RE, Clark SD, Schaeffer J, Boothe DL (2004) Evaluation of the residual benefits of boron fertilization on soybean and rice. In: Wayne E. Sabbe (Ed.) *Arkansas soil fertility studies*. AAES Res Series Arkansas Agricultural Experiment Station. Division of Agriculture, University of Arkansas, Fayetteville, USA, 525:100–104
- Small HG, Ohlrogge AJ (1973) Plant analysis as an aid in fertilizing soybeans and peanuts. In: Walsh LM, Beaton JD (eds) *Soil testing and plant analysis*. Soil Science Society of America, Madison, pp 315–327
- Smithson JB, Heathcote RG (1976) A new recommendation for the application of boronated superphosphate to cotton in northeastern Beune Plateau States. *Samarau Agri Newsletter* 18:59–63
- Sonmez O, Aydemir S, Kaya C (2009) Mitigation effects of mycorrhiza on boron toxicity in wheat (*Triticum durum*) plants. *New Zeal J Crop Hort Sci* 37:99–104

- Sprague HB (1951) Hunger signs in crops, 3rd edn. McKay, New York, pp 25–57
- Sprague RW (1972) The ecological significance of boron. United States Borax and Chemical Corp, Los Angeles, p 58
- Stuerz S, Sow A, Muller B, Manneh B, Asch F (2014) Canopy microclimate and gas exchange in response to irrigation system in lowland rice in the Sahel. *Field Crops Res* 163:64–73
- Sulaiman W, Kay BD (1972) Measurement of the diffusion coefficient of boron in soil using a single cell technique. *Soil Sci Soc Am Proc* 36: 746–752
- Swarup A (1991) Effect of gypsum, green manure, FYM and zinc fertilization on the zinc, iron and manganese nutrition of wetland rice on a sodic soil. *J Indian Soc Soil Sci* 39:530–536
- Takano J, Noguchi K, Yasumori M, Kobayashi M, Gajdos Z, Miwa K, Hayashi H, Yoneyama T, Fujiwara T (2002) Arabidopsis boron transporter for xylem loading. *Nature* 420:337–340. <https://doi.org/10.1038/nature01139>
- Takano J, Miwa K, Yuan L, von Wiren N, Fujiwara T (2005) Endocytosis and degradation of BOR1, a boron transporter of *Arabidopsis thaliana*, regulated by boron availability. *Proc Natl Acad Sci* 102: 12276–12281. <https://doi.org/10.1073/pnas.0502060102>
- Tanaka H (1967) Boron absorption by crop plants as affected by other nutrients of the medium. *Soil Sci Plant Nutr* 13:41–44
- Tanaka M, Fujiwara T (2008) Physiological roles and transport mechanisms of boron: perspectives from plants. *Pflügers Arch - Eur J Physiol* 456:671–677. <https://doi.org/10.1007/s00424-007-0370-8>
- Tanaka N, Uruguchi S, Saito A, Kajikawa M, Kasai K, Sato Y, Nagamura Y, Fujiwara T (2013) Roles of pollen-specific boron efflux transporter, OsBOR4, in the rice fertilization process. *Plant Cell Physiol* 54:2011–2019
- Tariq M, Mott CJB (2007) Effect of boron on the behavior of nutrients in soil-plant systems—a review. *Asian J Plant Sci* 6:195–202
- Tisdale SL, Nelson WL, Beaton JD (1985) Soil fertility and fertilizers. Macmillan, New York
- Tsadilas CD, Yassoglou CS, Cosmas CS, Kallianou CH (1994) The availability of soil boron fractions to olive trees and barley and their relationships to soil properties. *Plant Soil* 162:211–217
- Tuong TP, Bouman BAM, Mortimer M (2005) More rice, less water: integrated approaches for increasing water productivity in irrigated rice-based systems in Asia. *Plant Prod Sci* 8:231–241
- Uraguchi S, Fujiwara T (2011) Significant contribution of boron stored in seeds to initial growth of rice seedlings. *Plant Soil* 340:435–442
- Van de Vender HA, Currier HB (1977) The effect of boron deficiency on callose formation and ^{14}C translocation in bean (*Phaseolus vulgaris* L.) and cotton (*Gossypium hirsutum* L.). *Am J Bot* 64:861–865
- Wang K, Xu JM, Wei YZ, Yang Y, Bell RW (1997) The influence of boron fertilizer on distribution of extractable boron in soil profiles in rape-rice rotations in south east China. In: Bell RW, Rerkasem B (eds) Boron in soils and plants. Development in plant and soil sciences, vol 76. Kluwer Academic, Dordrecht, pp 57–61
- Wang K, Yang Y, Bell RW, Xue JM, Ye ZQ, Wei YZ (1999) Low risks of toxicity from boron fertiliser in oilseed rape-rice rotations in south-east China. *Nut Cycl Agroecosyst* 54:189–197
- Wang Q, Lu L, Wu X, Li Y, Lin J (2003) Boron influences pollen germination and pollen tube growth in *Picea meyeri*. *Tree Physiol* 23: 345–351
- Wang Y, Shi L, Cao X, Xu F (2007) Plant boron nutrition and boron fertilization in China. In: Xu F, Goldbach HE, Brown PH, Bell RW, Fujiwara T, Hunt CD, Goldberg S, Shi L (eds) Advances in plant and animal boron nutrition. Springer Netherlands, pp 93–101
- Warington K (1933) The influence of length of day on the response of plants to boron. *Ann Bot* 47:429
- Wear JJ, Patterson RM (1962) Effect of soil pH and texture on the availability of water-soluble boron in the soil. *Soil Sci Soc Am Proc* 26: 344–346
- Weir RG, Cresswell GC (1994) Plant nutrient disorders: 4. Pastures and field crops. Inkata, Melbourne
- Welch RM, Allaway WH, House WA, Kubota J (1991) Geographic distribution of trace element problems. In: Mortvedt JJ, Giordano PM, Lindsay WL (eds) Micronutrients in agriculture. Soil Science Society of America, Madison, pp 31–57
- Westmark PR, Gardiner SJ, Smith BD (1996) Selective monosaccharide transport through lipid bilayers using boronic acid carriers. *J Am Chem Soc* 118:11093–11100
- Wimmer MA, Eichert T (2013) Mechanisms for boron deficiency-mediated changes in plant water relations. *Plant Sci* 203:25–32
- Wimmer M, Mühling KH, Läuchli A, Brown P, Goldbach HE (2003) The interaction between salinity and boron toxicity affects the subcellular distribution of ions and proteins in wheat leaves. *Plant Cell Environ* 26:1267–1274
- Wimmer MA, Lochnit G, Bassil E, Mühling KH, Goldbach HE (2009) Membrane-associated, boron-interacting proteins isolated by boronate affinity chromatography. *Plant Cell Physiol* 50:1292–1304
- Witt C, Cassman KG, Olk DC, Biker U, Liboon SP, Samson MI, Ottow JC (2000) Crop rotation and residue management effects on carbon sequestration, nitrogen cycling and productivity of irrigated rice systems. *Plant Soil* 225:263–278
- Xu JM, Wang K, Bell RW, Yang YA, Huang LB (2001) Soil boron fractions and their relationship to soil properties. *Soil Sci Am J* 65: 133–138
- Yang XD, Sun SQ, Li YQ (1999) Boron deficiency causes changes in the distribution of major polysaccharides of pollen tube wall. *Acta Bot Sin* 41:1169–1176
- Yang X, Yu YG, Yang Y, Bell RW, Ye ZQ (2000) Residual effectiveness of boron fertilizer for oilseed rape in intensively cropped rice-based rotations. *Nutri Cycl Agroecosyst* 57:171–181. <https://doi.org/10.1023/A:1009837120062>
- Yau SK (1997) Differential responses of barley, durum and bread wheat to high levels of soil boron. In: Ryan J (ed) Accomplishments and future challenges in dryland soil fertility research in the Mediterranean area. International Center for Agricultural Research in the Dry Areas, Aleppo, pp 209–216
- Ye Z (2004) Effect of low temperature on boron nutrition of oilseed rape and sunflower (Doctoral dissertation, Murdoch University)
- Ye Z (2005) Effect of low temperature on plant boron nutrition. PhD thesis, Murdoch University
- Yermiyahu U, Keren R, Chen Y (1988) Boron sorption on composted organic matter. *Soil Sci Soc Am J* 52:1309–1313
- Yermiyahu U, Keren R, Chen Y (1995) Boron sorption by soil in the presence of composted organic matter. *Soil Sci Soc Am J* 59: 405–409
- Yermiyahu U, Ben-Gal A, Keren R, Reid RJ (2008) Combined effect of salinity and excess boron on plant growth and yield. *Plant Soil* 304: 73–87
- Yoshinari A, Takano J (2017) Insights into the mechanisms underlying boron homeostasis in plants. *Front Plant Sci* 8:1951
- Yu X, Bell PF (2002) Boron and lime effects on yield and deficiency symptoms of rice grown in greenhouse on acid typical glossoqualf. *J Plant Nutr* 25:2591–2602. <https://doi.org/10.1081/PLN-120015524>
- Zehirov GT, Georgiev GI (2003) Effects of boron starvation on the apoplastic and total solute concentrations influencing nodule growth and acetylene reduction rate. *Bulg J Plant Physiol* 29: 367–373