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REVIEW ARTICLE

Boron nutrition of rice in different production systems. A review

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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

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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

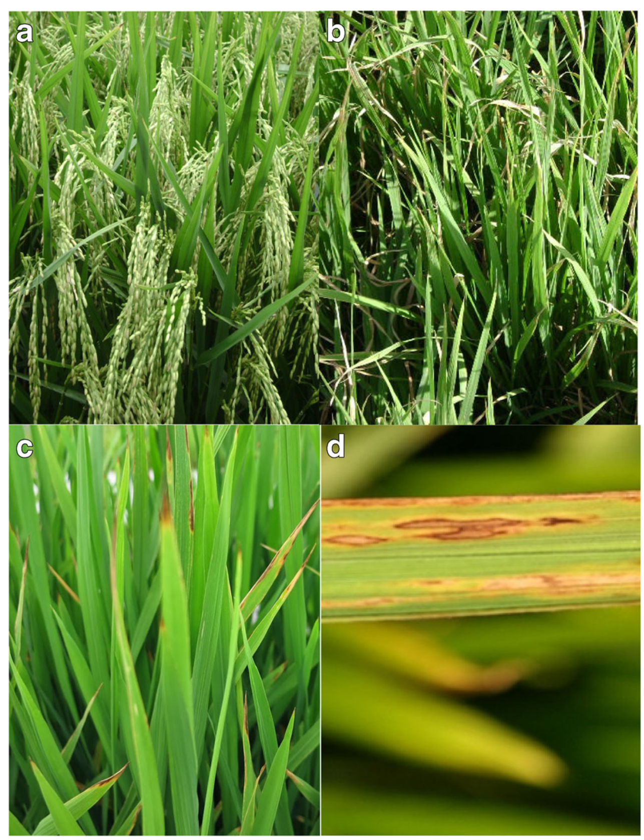

Fig. 1 Boron nutrition in rice. **a** Adequate boron. **b**, **c** Boron deficiency (interveinal chlorosis and necrotic spots). **d** Boron toxicity

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 Römheld 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-derythrofuranose 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 Römheld 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

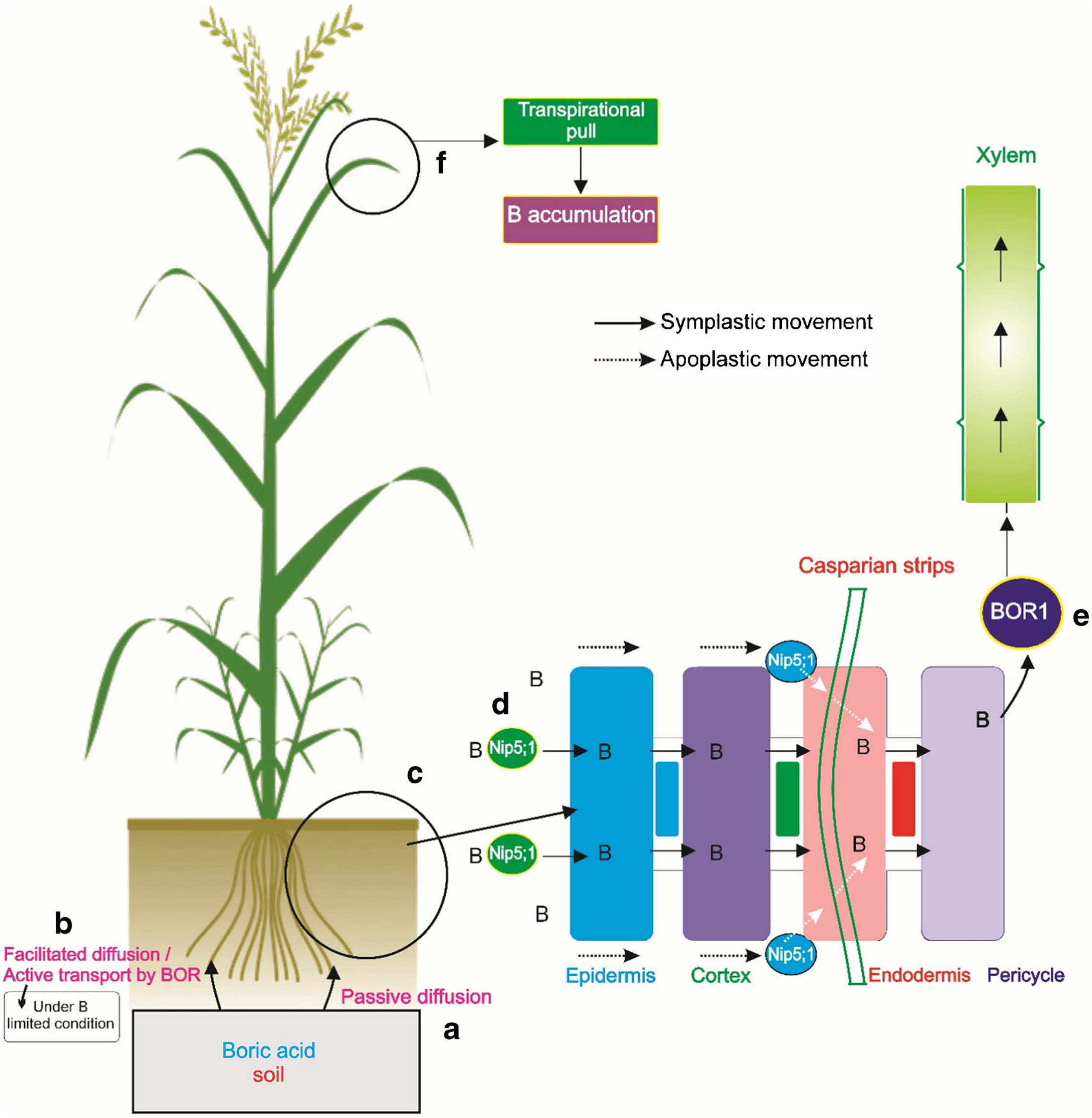

Fig. 2 Mechanism of boron (B) movement from soil to plant. (a) B is taken up by plant from the soil as 'boric acid,' an uncharged molecule. Under conditions of optimum availability, B is taken up by plants via passive diffusion. (b) Under B-deficient conditions, B movement occurs through active transport 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 Römheld 1997). Boron deficiency results in membrane leakage due to a loss of membrane functional integrity (Cakmak and Römheld 1997). Adequate supply of B may stimulate plasma membrane H^+-pumping activity by increasing the driving force for K^+ influx (Cakmak and Römheld 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 stomal frequencies and smaller stomatal apertures, which both reduce stomatal conductance to CO_2 (Sharma and Ramchandra 1990). Moreover, B deficiency disrupts chloroplast structure and the functioning of chloroplast thylakoids that restrict CO_2 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; Uraguchi 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; Uraguchi 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). Grassy have small amounts of pectin monocots 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 (H_3BO_3) 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 $H_2BO_3^-$ 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 Fe^{3+} to Fe^{2+} 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 pH < 7, $B(OH)_3$ dominates and the amount of B adsorption by the soil becomes small due to less fixation, and (2) as pH increases above 7.5, $B(OH)_4^-$ becomes increasingly prevalent and clay minerals have a relatively strong affinity for $B(OH)_4^-$, 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 (0.10–0.45 μg 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 p*K*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 rhamnogalacturonan 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 (Binghum 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 alumnosilicate clay minerals (Jasmund and Lindner 1973; Keren and Talpaz 1984; Mattigod et al. 1985). Boron in soluble and adsorbed forms remains in equilibrium (Binghum 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 (Sillanpaa 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 μmol m^{-2} 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 activeAI-2 that indicates its potential biological role for B (Chen et al. 2002). The AI-2 molecule is a furanosyl boratediester 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 ($Na_2B_4O_7{\cdot}10H_2O$), boric acid (H_3BO_3), sodium tetraborate ($Na_2B_4O_7{\cdot}5H_2O$), sodium pentaborate ($Na_2B_{10}O_{16}{\cdot}10H_2O$), and *Solubor* ($Na_2B_8O_{13}{\cdot}4H_2O$); and (ii) crushed minerals including ascharite ($2MgO{\cdot}B_2O_3{\cdot}H_2O$), colemanite ($Ca_2B_6O_{11}{\cdot}5H_2O$), datolite ($2CaO{\cdot}B_2O_3{\cdot}2SiO_2{\cdot}H_2O$), hydroboracite ($CaO{\cdot}MgO{\cdot}3B_2O_3{\cdot}6H_2O$), 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	3.89	5.88b	14b	20.1	8.5a	2.51b	34.0b	1.68
	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	4.72b	6.63b	16b	16.1	8.2b	2.49b	35.2b	1.78
	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	2.80
	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	
	1	5.48a	13.30a	12b	15a	8.3a	2.58a	69.6a	3.40
	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 $p \leq 0.05$

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·5B_2O_3·16H_2O) (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 $CaCl_2$ -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 $CaCl_2$-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
$Na_2B_4O_7{\cdot}10H_2O$	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_3BO_3	4.4	At transplanting	Flooding in pot	Silt loam	4.8	11	–	11.3 (7.1)*	USA	Yu and Bell (2002)
$Na_2B_4O_7{\cdot}5H_2O$	1.12	Basal dose	Direct seeding in aerobic culture	Silt loam	6.3	0	–	6.3 (6.1)	USA	Slaton et al. (2004)
$Na_2B_4O_7{\cdot}5H_2O$	2.24	Basal dose	Direct seeding in aerobic culture	Silt loam	6.3	2	–	6.4 (6.1)	USA	Slaton et al. (2004)
$Na_2B_4O_7{\cdot}5H_2O$	4.48[1]	Basal dose	Direct seeding in aerobic culture	Silt loam	6.3	0	–	6.2 (6.1)	USA	Slaton et al. (2004)
$Na_2B_4O_7{\cdot}5H_2O$	6.73[1]	Basal dose	Direct seeding in aerobic culture	Silt loam	6.3	0	–	7.2 (6.1)	USA	Slaton et al. (2004)
$Na_2B_4O_7{\cdot}10H_2O$	8.97[1]	Basal dose	Direct seeding in aerobic culture	Silt loam	6.3	0	–	7.2 (6.1)	USA	Slaton et al. (2004)
$Na_2B_4O_7{\cdot}10H_2O$	1.00	At transplanting	Conventional flooding	Silt loam	7.9–8.8	25	–	8.2 (5.3)	Pakistan	Rashid et al. (2004)
H_3BO_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)
$Na_2B_4O_7{\cdot}10H_2O$	1.00	At transplanting	Conventional flooding	–	7.4–8.4	31	–	–	Pakistan	Ahmad and Irshad (2011)
$Na_2B_4O_7{\cdot}10H_2O$	1.00–3.00	At transplanting	Conventional flooding	Silty clay loam	7.0	17–28	56–89 in grain	–	Malaysia	Saleem et al. (2011b)
$Ca_2B_6O_{11}{\cdot}5H_2O$ (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)
$Ca_2B_6O_{11}{\cdot}5H_2O$ (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_3BO_3	0.50–0.75	At transplanting	Conventional flooding	Clay loam	7.7	8–17	–	–	Pakistan	Shah et al. (2011)
$Na_2B_4O_7{\cdot}10H_2O$	1.50	At transplanting	Conventional flooding	Silty clay	8.0	13	–	–	Pakistan	Hussain et al. (2012)
$Na_2B_4O_7{\cdot}10H_2O$	1.50	At tillering	Conventional flooding	Silty clay	8.0	14	–	–	Pakistan	Hussain et al. (2012)
$Na_2B_4O_7{\cdot}10H_2O$	1.50	At flowering	Conventional flooding	Silty clay	8.0	20	–	–	Pakistan	Hussain et al. (2012)
$Na_2B_4O_7{\cdot}10H_2O$	1.50	At grain formation	Conventional flooding	Silty clay	8.0	14	–	–	Pakistan	Hussain et al. (2012)
H_3BO_3	2.00	At transplanting	Conventional flooding	Clay	8.11	53	–	–	Pakistan	Abbas et al. (2013)
$Ca_2B_6O_{11}{\cdot}5H_2O$ (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
$Ca_2B_6O_{11}\cdot 5H_2O$ (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_3BO_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_3BO_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_3BO_3	1.00	At transplanting	Conventional flooding	Sandy loam	8.2	22–40	23–39 in grain	–	Pakistan	Rehman et al. (2014a, 2016)
H_3BO_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)
$Na_2B_4O_7\cdot 10H_2O$	7.50	Basal dose	Direct seeding in aerobic culture	Silt clay	7.9	11	–	–	Pakistan	Sarwar et al. (2016)
$Na_2B_4O_7\cdot 10H_2O$	7.50	Basal dose	Alternate wetting and drying	Silt clay	7.9	3	–	–	Pakistan	Sarwar et al. (2016)
$Na_2B_4O_7\cdot 10H_2O$	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_3BO_3	Foliar application	200 mM	Alternate wetting and drying	Sandy loam	8.2	10–19	60–62	Pakistan	Rehman et al. (2014b, 2016)
H_3BO_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_3BO_3	Foliar application	200 mM	Conventional flooding	Sandy loam	8.2	23–46	29–35	Pakistan	Rehman et al. (2014b, 2016)
$Na_2B_8O_{13}·4H_2O$	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_3BO_3	Foliar application	0.2–0.8 ppm	Conventional flooding	Clay	8.1	3–10	–	India	Rao et al. (2013)
H_3BO_3	Foliar application	0.2–0.8 ppm	Conventional flooding	Sandy loam	4.6	20	–	India	Rao et al. (2013)
H_3BO_3	Foliar application	0.2–0.8 ppm	Conventional flooding	Sandy silty	7.2	8–13	–	India	Rao et al. (2013)
H_3BO_3	Foliar application	0.2–0.8 ppm	Conventional flooding	Silty loam	8.0	0	–	India	Rao et al. (2013)
H_3BO_3	Foliar application	0.2–0.8 ppm	Conventional flooding	Sandy clay loam	6.8	4–9	–	India	Rao et al. (2013)
H_3BO_3	Foliar application	0.2–0.8 ppm	Conventional flooding	Silty clay	5.5	3–4	–	India	Rao et al. (2013)
$Na_2B_4O_7·10H_2O$	Foliar application	1.5% B solution	Conventional flooding	Silty clay	8.0	8–10	–	Pakistan	Hussain et al. (2012)
H_3BO_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_3BO_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_3BO_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_3BO_3	Seed priming	0.1 mM	Conventional flooding	Sandy loam	8.2	18–27	26–36	Pakistan	Rehman et al. (2014b, 2016)
H_3BO_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)
$Na_2B_4O_7·10H_2O$	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 1.1–1.65 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 @ 1.1–3.3 kg B ha^{-1}	Wetland rice	Silty	6.5	0.81–3.23	China	Yang et al. (2000)
B fertilizer	Rape @ 1.1–3.3 kg B ha^{-1}	Wetland rice	Clay	5.1	2.61–3.48	China	Yang et al. (2000)
B fertilizer	Rape @ 1.1–3.3 kg B ha^{-1}	Wetland rice	Sandy	5.1	0.38–4.25	China	Yang et al. (2000)
B fertilizer	Rape @ 1.1–3.3 kg B ha^{-1}	Upland rice	Clay	6.4	1.24	China	Yang et al. (2000)
$Na_2B_4O_7{\cdot}5H_2O$	Soybean @ 1.12–8.96 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	*N*	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 8×10^{-6} 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.

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