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Boron: An Essential Element Needs Attention

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The number of elements considered essential for the growth of higher plants varies from 16 to 20 depending upon the definition of essentiality. According to Arnon (1943) essential elements are those which are needed for higher plants to complete all life functions and that the deficiency can be corrected by the application of this specific element causing the deficiency. Contrary to this Nicholas (1961) believe that an element should be considered essential if its addition enhances plant growth even though it merely substitutes for one of the 16 elements that Arnon declares to be essential. On the basis of the criteria used, Arnon specifies 16 elements and Nicholas 20 elements as being essential for the growth of higher plants. Beyond discussion and debate boron is considered as an essential element which has tremendous roles in plant growth and development, physiology as well as biochemical composition. For example, it helps to main balance between sugar and starch, translocation of sugar and carbohydrates, pollination and seed reproduction, cell division, nitrogen metabolism, protein formation as well as cell wall formation etc. In view of its role in plant processes and work done, more emphasis on research and applications of boron would help to improve crop productivity in a sustainable manner. In the present paper work done in relation to various functions of boron has been reviewed.

Keywords: Boron, deficiency, uptake, metabolism, yield.

INTRODUCTION

The element boron is unique among all the essential elements because in case of boron the gap between sufficiency and toxicity level is very narrow. A fraction of one part per million may be required, a few parts per million may be toxic to plants. It is absorbed from the soil by plants as borate, a negatively charged ion (anion). Since boron is non-mobile in plants, a continuous supply from soil or planting media is required in all plant meristems. In soils, release of boron is usually quite slow. Much of the available soil boron is held rather tightly by soil organic material. After decomposition of soil organic matter boron is released with a portion being absorbed by plants, leached below the root zone area (especially in high rainfall/acid soil areas) or tied up (unavailable) under alkaline soil conditions. Agulhon (1910) was the first to suspect B as an essential nutrient in plants, although probably on a wrong experimental ground as stated by Loomis and Durst (1991, 1992). Warrington (1923) was the first to really prove the essentiality of boron. Boron is most electronegative element in group III of periodic table. Its properties are intermediate between metals and electronegative non-metals. It has one less valence electron than number of valence orbital, which causes an 'electron deficiency' that has a dominant effect on the behavior of boron in chemical processes (Kot 2009). Chemical properties of boron as following:

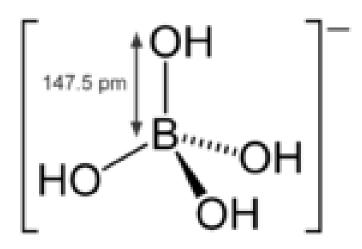


Figure 1. The structure of the tetrahydroxyborate anion

Atomic number	5
Element symbol	В
Relative atomic mass	10.8111
Melting point	2079 °C
Boiling point	2550 °C
Electronegativity (Allred, Rochow)	2.0
Oxidative state	3
Electron configuration	He 2s ² 2p ²

Boron deficiency in plants:

Boron is involved in many biochemical and physiochemical processes for optimal plant growth, its requirement vary markedly with crop plants (Shelp 1993). Several deficiency symptoms in different crops have been reported (Bussler 1979; Bergman and Newbert 1988; Bergmann 1983; Gupta 1979, 1983; Loomis and Durst 1991, 1992; Shelp 1993). Deficiencies of boron are emerged because of intensive cropping, use of high analysis fertilizer and adoption of high yielding varieties (Rafique et al., 2006). Some characteristic deficiency symptoms of boron in different plant parts comprise:

i. For roots: Inhibits root growth sometimes within 3 to 6 hours, thickening of roots giving a coral - like shape, inhibited rooting of cuttings (Ali and Jarvis, 1988) browning of tissues especially of root apex, cracking of root tissues, altered cell walls, inhibited apical and extension growth.

ii. For shoots: Inhibited apical and extension growth, browning and necrosis of apical tissue such as black heart in sugar beets, die back, altered cell walls, cracking and breaking of stem and petioles.

iii. For reproductive organs: Delay or prevention of flowering, dehiscence of flowers or fruits, sterile flowers,

inhibited pollen tube growth or bursting of pollen tubes, bronzing and fruit deformation reduced fruit size (Goldbach, 1997).

Boron deficiency has been reported to inhibit nucleic acid synthesis (Albert 1975), enhances RNase activity (Champman and Jacknson, 1974), increase carbohydrate contents (Shkol'nik, 1984), inhibits photo and oxidative phosphorlyation (Eichhorn and Augsten 1974), starch accumulation (Agier et al., 1982) inhibition of trans membrane transport (Coke and Whittington, 1968) and ATPase activity (Heyes et al., 1991) reduced leaf area along with the content of chlorophyll in leaves (Kostori et al., 1995).

Uptake and distribution of boron in plants

Boron seems to be taken up mainly as undissociated boric acid (Bingham et al., 1979, Ortli and Grgurevic 1975) or as borate anion (Bowen 1968). Bowen and Nissen (1976) suspected an active, carrier mediate mechanism which was justified by Ortli and Grgurevic (1975). Ortli and Grgurevic (1975) found that the uptake of boron was reduced at increasing pH values, i.e., with increasing borate concentrations, which indicates that more borate esters may be retained in the apoplastic space and/or that the uptake of the borate anion is inhibited.

Depending on availability of boron boron transport can be performed by either of three ways: (i) Passive transport across the plasmalemma mediated by simple diffusion when adequate or excessive boron is available in the soil (ii) Energy dependent high-affinity transport, it is induced in response to low boron supply, it is mediated via BOR transporters and (iii) Facilitated transport carried out by

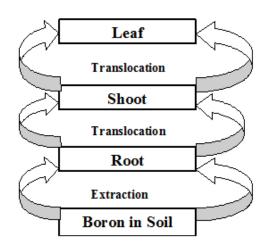


Figure 2. Translocation of boron in plants

NIP channel proteins (Tanaka and Fujiwara, 2008).

There is still some controversy on the translocation of boron in plants. Ziegler (1975) assumed that boron is completely phloem immobile as it would damage the sieve tubes. Dugger (1983), too denied a mobility of boron in the phloem. It is generally accepted that most of the boron taken up from the soil (if not all) is translocated via xylem (Kohl and Oertil, 1961; Rave, 1980).

Bussler and Doring (1979) reported the occurrence of a significant concentration of boron in chloroplasts, which became proportionally higher under boron deficiency (i.e., the amount of boron in this fraction was reduced less). This suggests a role for boron in photosynthesis. Boron application significantly increases the leaf tissue B concentration in potato (Gupta and Sanderson, 1993). Lowrence et al. (1995) reported that boron is essential for optimal function of plasma membrane ATPase and redox systems in chickpea. Boron presumably stabilizes the structures of the plasma membrane by complexing membrane constituents (Ismail et al., 1995). Matoh et al., (1996) reported that in all species examined cell wall boron was judged to be associated with rhamnogalacturonan II (RG-II). Moreover, in over 15 species it seemed likely that RG-II might be the exclusive carrier of boron in cell wall. B may fulfill its essential function forming the B-RG-II complex in cell walls (Kobayashi et al., 1996). In species in which sorbitol is a major sugar (sorbitol rich), B is freely mobile while in species that produce little or no sorbitol (sorbitol poor), B is largely immobile (Patrick and Hening, 1996). Increasing solution boron concentration in boron buffered solution increases boron concentration in roots (Asad et al., 1997).

Boron in relation to water relation

Available evidences show that boron regulates the water

relations in plants. The leaves of soybean (Minarik and Shive, 1939) and tobacco (Leaf, 1953) had a higher moisture content in boron deficiency than in normal plants. The decrease in water loss in boron deficiency has been attributed to the presence of higher concentration of hydrophilic colloids (Baker et al., 1956). In boron deficient leaves of cabbage a decrease in water potential, stomatal pore opening and transpiration rate and an increase in tissue hydration and lowering of water saturation deficit was observed (Sharma et al. 1984). Apart from this, in sunflower and mustard leaves, an increased diffusive resistance and decreased rate of transpiration, water potential and water saturation deficit was found (Sharma and Ramachandra 1989, 1990).

Physiological and biochemical roles of boron

I. Respiration: Boron deficiency results in a higher rate of O2 uptake in leaves or leaves extract of tomato. At the same time a decrease in respiratory phosphorylation in boron deficient sunflower tissue was also reported (Timashov 1970). When boron is in excess supply, it suppresses the oxygen evolution and respiratory oxygen uptake (Ahmed et al. 1988).

II. Carbohydrate metabolism: Boron plays an important role in the carbohydrate metabolism. In several crops deficient in boron, total and reducing sugars are known to accumulate either in leaves or in roots (Agarwala et al. 1978). Accumulation of starch in boron deficient condition in several plant species have also been reported, viz., in beans (Dvorinc et al. 1972), Lemna minor (Dugger 1983) and mustard (Sharma and Ramchandra 1990). Boron supply improves the seed quality in respect to protein, fat and carbohydrate concentration (Gaina and Silli 1973), foliar spray of boron at reproductive stage in boron deficient sorghum

increases the water soluble sugars of seed coatings (Misra et al. 1991). Previous studies indicate involvement of boron in sugar metabolism (Marschner 1995), especially sugar alcohols (Bellaloui et al. 1999). In plants, boron is known to play important roles in structure of cellwalls, membranes and membrane associated reaction. It is involved in cell membrane integrity (Schon and Blevins, 1990) and cell wall structure (Brown et al. 2002).

III. Nitrogen metabolism: Lee et al., (1990) reported increased N uptake and N- fixation by application of gypsum and trace elements including B in inoculated seedling of groundnut. Mo, B application tended to increase seed N content at flowering. N contents were highest in leaves and lowest in roots (Pasypanov and Zherukov, 1992). In pea roots increase in non-protein nitrogen was, attributed to the decrease in the rate of protein synthesis in boron deficiency (Rapata 1970) and increased concentration of free amino acid (Agarwala et al. 1978, Pe dash and Sereda 1985). Boron supply to boron deficient soils increased protein N absorption and transformation of nitrogen, nodulation and N2 fixation in red clover root (Ma et al. 1990). In deficiency and toxicity of boron, in sugarbeet and sunflower roots and shoots, a marked accumulation in nitrate and decrease in nitrate reductase activity was noticed (Bonilla et al., 1980). Boron plays an indispensable role in nodule formation, nitrogen fixation and nitrogen assimilation in grain legumes of soybean (Srivastave et al., 1982). Absence of boron in culture medium resulted in a decrease of the number of nodules and an alteration of nodule development leading to an inhibition of nitrogenase activity (Bolanos et al. 1994). This is also an essential micronutrient for the development of nitrogen fixing root nodules in pea (Pisum sativum) (Luis et al. 1996).

IV. Phenolic compounds: Lee and Aronoff (1967) suggested a role of boron as borate in partitioning and metabolism between glycolytic and pentose shunt pathway. The inhibition of growth of the plant in boron deficiency has been attributed to the accumulation of phenolic compounds (Shko'nik 1974). Boron plays an important role in xylem formation and lignification (Skok, 1958). Loomis and Durst (1992) pointed out that boron deficiency reactions occur during the growth of primary wall at a stage where there is still no lignification at all. It is involved in phenolic metabolism (Bellaloui et al. 2012).

V. Nucleic acids: Krueger et al. (1987) found an inhibition of DNA synthesis (reduced incorporation of ³H - thymidine) as short as 6 hours after transfer to boron deficient condition. Boron toxicity (in part) hampers protein synthesis by borate ester formation with ribose (Loomis and Durst 1991, 1992). Boron acts by forming a strong positive electrostatic charge in the membrane through the capture of an electron loosen from donor. The positive charge could attract and orient negatively charged molecules, such as nucleic acids and thereby initiate, facilitate or control certain vital reactions involved

in cell division, cell elongation and flowering (Tanada, 1995) and nucleic acid metabolism (Dordas and Brown, 2000).

VI. Enzymes: Boron is not reported to be an integral part of any enzyme protein but there are several reports that it influences the activity of many enzymes. Treatment of corn seeds with 0.001% H₃BO₃ enhanced the activity of nitrate reductase, starch phosphorylase and polyphenol oxidase (Chatterjee et al., 1990). It inhibits the activity of lipoxinase in 6 day old sunflower cotyledons (Belver and Donaire, 1983).

Role of boron in reproductive physiology: Boron VII. plays an important role in the development of reproductive parts in plants. Generally, the concentration of boron in plants in comparatively higher in flower, anthers, ovary and stigma (Gauch and Dugger, 1954). Symptoms such as spikelet sterility in wheat and rosetting in radish and cabbage, suggested to boron as a probable factor involved in the abortion of flowers and failure of pod set in chickpea (Srivastava et al., 1996). In Larix deciduas Mill., suspensor development was found to be dependent on boron concentration, below 35 mM boron, suspensor formation was blocked completely whereas with an increase upto 1mM boron there is progressively faster development of suspensor bearing embryos (Ulrike and Zoglaver, 1996).

VIII. Role of boron in improving yield

Boron deficiency does not reduce the number of seeds/ fruits per plant but reduces the weight, diameter, reducing sugar contents. Application of boron was found to increase fruit weight and sugar accumulation in fruits like tomatoes. Foliar spray of boric acid at bud formation stage increased the seed yield in Lucerne (Krivoshei and Kononovich, 1978) and red clover (Eriksson, 1979). Foliar application of boron at the end of flowering has been reported to increase 100 seed weight in soybean (Radeva et al. 1991). Pod length and pod number per plant in P. vulgaris and fruit weight per plant in tomato increased with the increasing concentration of boron in solution (Coetzer et al. 1990). Boron application was found to increase the yield of different crops (Dwivedi et al. 1990). Foliar application of Boron at reproductive stage was found to enhance grain yield and different yield components of wheat (Ahmad and Irshad, 2011). Kandi et al. (2012) found that foliar application of B on safflower plant had the highest positive effect on plant biological vield, harvest index and seed boron content. It is an essential nutrient for plant growth, development, and seed quality (Dordas et al., 2007). An enhancement in the productivity was found by greater assimilation of boron and resulting positive effects on components contributing to yield (Ali et al. 2013).

Interaction of boron with other nutrients

Boron deficiency has been reported to decrease the zinc

concentration in cotton (Ohki, 1975) and its uptake in tomato (Alvarez-Tinaut et al. 1979). Zinc concentration increases with the development of boron toxicity in the leaves. Zinc application decreases the boron content and high rates of boron decreases the zinc content particularly in shoot.

CONCLUSION

Optimum plant growth response can be achieved by making sure that plants are provided a reasonable supply of all essential elements. With many soils, conditions are conducive to low soil levels of boron. By including soil testing for boron, deficiencies or toxicities can be identified and corrected to attain maximum yield potential of crops. A little boron goes a long way in preventing deficiencies or creating toxicities. Although it has several key roles in plant growth and metabolism but so for problems have not been addressed properly. Hence, there is a need to focus researches on roles of boron on different metabolic processes as well as on different crops. In addition, it is needed to commercially produce boron for application in agri-horticulture. Besides its application in annual crops application of boron may play crucial role in perennial horticultural crops. Although, some work has been done on vegetables which are mostly annuals, research in relation to its application on fruit crops is still need attention. This is a fertile area of research which is so far unexplored. Being a micronutrient small amount of boron may be conducive in improving production and productivity which will be economical for farmers. Hence, in future in depth research on impact of boron application on different plant processes will help to improve crop productivity in a sustainable and farmer friendly manner.

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