BORON 2 (3), 175 - 183, 2017

BOR DERGİSİ
JOURNAL OF BORON
http://dergipark.gov.tr/boron

# Mobility and distribution of boron in plants and effects on reproductive growth and yield

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## ARTICLE INFO

**Article history:**
Received 29 September 2017
Received in revised form 27 December 2017
Accepted 27 December 2017
Available online 30 December 2017

**Review Article**

**Keywords**:
Boron-complexing,
Boron requirements,
Cell wall,
Deficiency symptoms
Pectin,
RG-II,
Sugar alcohols

## ABSTRACT

Most boron (B) behaviour in plants can be explained by complexation of B in cell walls and membranes which links the consequences of B deficiency to the disruption of cell wall and membrane function. Many symptoms of B deficiency reflect the localised and timely need for B for stabilisation of cell walls in tissues with expanding cells, e.g. flowers, fruit, root tips and shoot meristems. The internal B requirement of tissues for adequate function is determined by the abundance of rhamnogalacturonan-II (RG-II) which complexes B in the cell wall. Reproductive plant parts appear to be particularly at risk from low B supply, in part because they require relatively high concentrations of B compared to vegetative tissues. When external B concentrations are adequate to high, the uptake and distribution of B in plants can be largely explained by the uptake of water and its movement within the plant. However, under marginal and deficient external B concentrations, channels and transporters exert significant control of the uptake and distribution of B within the plant. Channels and transporters in roots promote uptake and loading of B into the xylem. For flowers, pollen and seed, with low rates of transpiration, channels and transporters are probably involved in their B acquisition under low external supply. The mobility of B in the phloem is variable among species. In most plants, B is immobile in the phloem and growing tissues rely substantially on B supplied through the xylem or by xylem-to-phloem transfer. However, if present in the phloem, B-complexing compounds, notably sugar alcohols, allow free mobility of B in the phloem so that B can be retranslocated within the plant of those species especially under deficient supply.

## 1. Introduction

Significant new insights have emerged into plant boron (B) nutrition in the last two decades which have elucidated the essential role of B in plants, and shed light on the regulation of B mobility and distribution in plants [1-4]. Considering the factors affecting B distribution in plants, it has been necessary to re-think the influence of: variable B requirements for the assembly of the expanding cell wall; active *vs* passive B uptake; variability amongst plant species and cultivars in B remobilisation and retranslocation; and B channels and transporters.

This review begins with an examination of the role of B in the cell wall and its relationship to B deficiency symptoms in plants, then it discusses several studies in which factors affecting B distribution were examined. The case studies examine effects of: B supply, growth rate of plants; shoot to root ratio; species and cultivar differences; transpiration rate of tissues, and; temperature. The aim of the review is to suggest directions for future research on factors affecting B distribution in plants, and identify strategies for improved management of B nutrition in crops in the field. The scope of the review is on deficiency of B supply rather than toxicity.

## 2. Boron essential for cell wall stabilisation

Deficiency of B can have either subtle or generalised effects on plant growth. But most of the symptoms can be attributed to the essential role of B in stabilising cell walls [5]. Boron forms bis-diol complexes with ramnogalactoruan (RG-II) which stabilise the pectin layer of the cell wall [6]. Curiously, while B has been claimed to be an essential element for higher plants since 1923 when reported by Warrington [7], it was only after the evidence of B complexation in RG-II that B satisfied the final criterion outlined by Epstein [8] for essentiality, namely that “the element is part of some essential plant constituent or metabolite”.

Many other putative roles of B have been suggested, but apart from its formation of a complex with RG-II that stabilises cell walls, few other roles have been sustained by critical evidence [9]. There is some evidence that B forms complexes in protein domains in the cell membrane [10]. The in-vitro formation of a

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*Corresponding author: R.Bell@murdoch.edu.au glycosylinositol phosphorylceramides-RG-II (GIPC-B-RG-II) complex, provides the first putative molecular explanation for wall-membrane attachment sites observed in vivo, and suggests a role for GIPCs in the RG-II dimerization process [11]. Withdrawal of B from the external solution can cause measurable changes in cell wall and cell membrane functions within minutes. Other roles attributed to B may be secondary effects of B deficiency impairment of the structure and function of cell walls and membranes, which in turn hampers meristematic growth, and the utilisation of carbon assimilates for new growth. Boric acid forms stable complexes with cis-diol and bis-diol moieties and any additional essential roles of B are most likely to be associated with those compounds that form stable or semi-stable complexes with B [9, 12].

## 3. Localised effects of B deficiency

Many symptoms of B deficiency reflect the localised need for relatively small amounts of B for stabilisation of cell walls in tissues with expanding cells, e.g. flowers, fruit, root tips, shoot growth zones. While the amount required at any tgiven ime for expanding cells is small, the timing of supply is critical and interruption of B supply to the expanding tissues can cause irreversible damage to the cell wall and a cascade of secondary and tertiary effects. Recent studies suggest that RG-II can form a di-ester with B during synthesis or during secretion into the cell wall but not once secreted into the cell wall [13]. This may explain the irreversible nature of many B deficiency symptoms that lead to distortion of stems, fruit, tubers or internal defects in the tissues.

When the symptoms predominantly are expressed in reproductive tissues, the symptoms can have quite localised and subtle direct effects on plant growth (Fig. 1A). Where the expression of B deficiency is predominantly in vegetative tissues, more generalised effects on plants are evident (Fig. 1B). In other species, such as oilseed rape and lentil (Fig. 1C and 1D), symptoms occur in either vegetative plant parts or reproductive plant parts depending on the timing and severity of B deficiency.

The B requirements of plant tissues vary widely. In vegetative tissues, the variation in leaf B concentrations can be explained by the uronic acid content of cell walls [14]. Graminaceae have low leaf B requirements due to low uronic acid content in cell walls. As a consequence, leaf elongation in wheat was only impaired by B concentrations < 1 mg B/kg [15]. By contrast in soybean, elongation of the youngest open leaf needed 10 -12 mg B/kg [16].

In general, the B concentrations required in reproductive plant parts exceed those in vegetative plant parts (Table 1). In Graminaceae, the B concentrations required to avoid deficiency symptoms in flowers are 5-10 fold higher than required in leaves. In dicotyledons, even through their leaf B requirements are higher than monocotyledons, the flowers have higher B requirement still.

There are many examples of very localised effects of B deficiency. Low B supply to black gram (*Vigna mungo*) for example had no negative effect on seed yield on a low B sand, but decreased seed B concentrations below 6 mg B/kg [17]. When the low B seed was imbibed, up to 25 % were non-viable and up to 60 % of the emerged seedlings grew abnormally with symptoms such as abortion of the epicotyl, one or both cotyledons or the primary root, or a shortened hypocotyl (Fig. 2). These defects were absent from germinating seedlings when seed had higher B concentrations. In the case of peanut and soybean, even where low B supply had no detrimental effect on seed yield, the low B seed were deformed resulting in symptoms, called hollow heart, on the inner surfaces of the cotyledon of peanut [18] or on the outer surface of the soybean seed [19, 20]. These B deficiency symptoms are restricted to specific parts of the seed and suggest that during seed development, B unloading into cells developing in either the embryo or the cotyledon was

**Table 1.** Boron concentration in plant parts exhibiting B deficiency symptoms

| Species | Plant part | B concentration in affected part (mg B/kg) | Source |
|---|---|---|---|
| Wheat | Youngest emerged leaf | <1 | [15] |
| | Ear at booting | 3-7 | [21] |
| | Carpels at booting | <6 | “ |
| | Anthers at anthesis | < 10 | [22] |
| Rice | Flag leaf | 3.2-3.3 | [23] |
| | Palea and lemma | 2.5-3.3 | “ |
| | Anther | < 20 | “ |
| Oilseed rape | Youngest open leaves | <10 | [24] |
| | Flowers and flower buds | 40 | [25] |
| Sunflower | Leaf | <20-25 | [25, 26] |

inadequate resulting in irreversible damage to the cell walls formed.

Wheat sterility is another example of very localised B deficiency, albeit with severely damaging effects on crop yield [27, 28]. The B requirement for leaf growth in wheat is extremely low. However, withdrawal of external B during young microspores stage of pollen development for even 3-5 days results in severe sterility (Fig 3; Table 2). The critical stage of pollen development during young microspore development [28] may last for no more than a few days in wheat

**Figure 1.** Boron deficiency symptoms: A. Profound growth depression in eucalyptus in Southern China in the foreground compared to the tall trees treated with B in the background. Photo credit: B. Dell; B. Subtle B deficiency in wheat in Bangladesh. Boron deficiency causes sterility of pollen and failure of grain set in the ear, but vegetative growth of the crop is unimpaired; C. Profound B deficiency in oilseed rape in Zhejiang Province China, causing severe stunting of plants and failure of most plants to flower or set pods (in centre of the photograph) compared to plants in either side with B fertiliser added; D. Profound and severe B deficiency in lentil in northern Bangladesh resulting in stunted plants, yellowing of young leaves and abortion of flowers.

**Figure 2.** Boron deficiency symptoms of seeds and germinated seedlings: A. on the internal face of the cotyledon of peanut (called hollow heart); B. as a dimple on the outer surface of soybean seeds; C. aborted epicotyl and; D. aborted primary roots of black gram seedlings after germination of low B seed.

grown in sub-tropical regions where B deficiency and wheat sterility are common [29]. Huang et al. [30] showed that withdrawal of B from the external solution during the young microspore stage induced pollen sterility of wheat in spring, but not for plants grown in the winter season.

Growth and development of reproductive plant parts appears to be particularly at risk from inadequate allocation of B to these tissues or to interruptions to B supply. The distinctive characteristic of B is the localised demand for B by all cells for a short period while the cell walls are expanding. Only concentrations < 2-3 mg B/kg impair maize leaf growth. By contrast, the minimum B requirement for maize pollen germination is 11 mg B/kg [31]. Similarly in rice, Lordkaew et al. [23] showed the anthers required > 30 mg B/kg to achieve maximum grain set and pollen viability.

The higher B requirement for pollen development may be attributed to greater pectin content in cell walls compared to leaf tissues. However, other factors may be involved. During the critical phase of pollen development of wheat for example, the ear is enclosed within leaf sheath and hence its water loss by transpiration is very limited which impairs the xylem supply of B to the pollen.

Moreover, in most plants, there is limited retranslocation of B in phloem so restriction of xylem supply of B to the developing pollen, flower or fruit can have severe effects on reproductive growth [27]; (Fig. 4). However, factors controlling B long distance and short distance transport to zones of expanding cells across a wide range of plant species are not well understood. Various factors affecting B distribution are discussed below: cultivars, growth rate, temperature, phloem mobility of B. In other cases, B deficiency damages the xylem vessels with consequences for B transport in the shoot [32].

In conclusion, the expression of plant B deficiency symptoms is quite revealing about B roles and function in plants. Firstly, primary deficiency occurs predominantly (perhaps exclusively) in rapidly growing tissues. Secondly, dicotyledons are more sensitive than monocotyledons to B deficiency on account of the higher B requirement in their cell walls that have a higher content of RG-II, the moiety that stabilizes the cell wall by formation of complexes in the pectin layer with boric acid. Thirdly reproductive tissue and fruits are frequently the most sensitive stage of growth for B deficiency. The extreme sensitivity of reproductive tissues to B deficiency can be attributed to the higher demand for B in their cell walls as a result of higher pectin content and to restricted delivery of B via xylem to non-transpiring organs. Fourthly, deficiencies can occur very quickly and be restricted to an highly

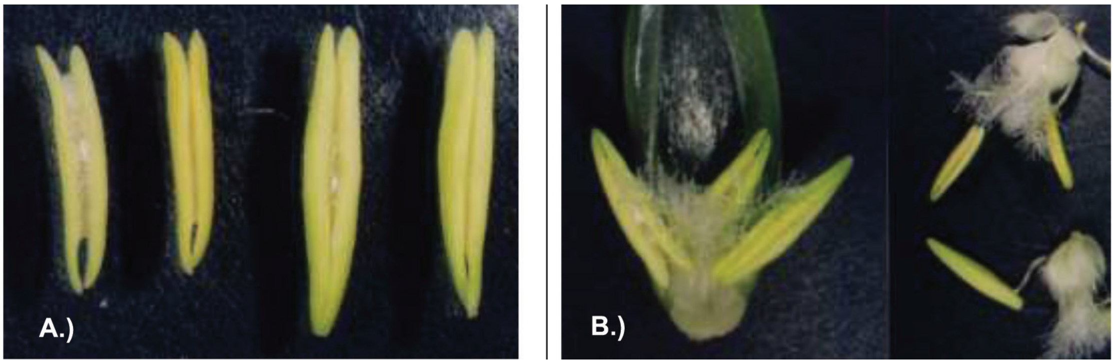

**Figure 3.** A: Withdrawal of external B supply for more than 3 days (anthers on the left compared to B-adequate anthers on the right) restricted elongation of the anther of wheat; B: Stunted size of wheat florets under B deficiency (right) compared to B-adequate florets (left). Photo credits: L. Huang

specific organ. Finally, chlorosis and necrosis occur as B deficiency symptoms in only a limited number of species and rarely as a first symptom. Symptoms such as yellowing and many reported roles of B are likely secondary or tertiary effects of the primary deficiency that impairs cell wall stabilization, and perhaps membrane function. In some plant species, leaf chlorosis is a symptom of B deficiency (e.g. lentil- see Figure 1). It is likely that oxidative damage causes leaf chlorosis in the B deficient plants of lentil (and some other species such as lucerne), but the primary cause of the increased activity of reactive oxygen species, that cause oxidative damage, is due to suppressed demand for assimilates due to the slow down in growth of newly-forming B-deficient tissues.

## 4. Boron distribution and redistribution

When external B concentrations are adequate to high, the uptake and distribution of B in plants can be largely explained by the uptake of water and its movement within the plant[4]. Highest B concentrations will accumulate in old leaves and in the tips and margins of old leaves. However, under marginal and deficient external B concentrations there is evidence of complex controls involving channels and transporters in the uptake and distribution of B within the plant [4]. Channels and transporters in roots promote uptake and loading of B into the xylem. Additional transporters are expressed in flowers, pollen and seed [33] which may explain how tissues with low rates of transpiration can acquire their B requirements under low external supply. In rice, the NIP3;1 channel is expressed in the nodal tissue of the stem which facilitates the transfer of B within the shoot away from the leaves that transpire most water to the expanding cell walls and meristems of leaves and the panicle [34].

Wheat is an interesting case for the transport of B into the reproductive tissues, since during its early development, the ear is entirely enclosed by one or more layers of leaf sheath that suppress transpirational water loss from the ear. Hence the direct transport of B in the xylem to the ear during this stage is likely to be minimal. Moreover, the ear is supplied with sugars from the phloem but not with water. The wheat ear is particularly sensitive to sterility due to interruptions of B supply to the ear [29]. To explore the role of transpiration in B partitioning into the ear of wheat, Huang et al. [35] applied a short term canopy cover of wheat plants and then determined the uptake of B into both the youngest emerged leaf and the ear. The canopy cover greatly suppressed leaf transpiration and decreased the amount of newly acquired $^{10}$B in both the flag leaf and the ear, but not in the upper stem segments. However, even with low external B concentrations, $^{11}$B continued

**Figure 4.** A. Boron deficiency of oilseed rape on low B soils in Zhejiang province, China. Abortion of flower buds was one of the B deficiency symptoms. B. Complete flower abortion of black gram. As a consequence of flower abortion and suppression of apical shoot growth, assimilates accumulated in existing plant parts, producing thickened petioles, stems and leaves (which were also very dark green).

to accumulate in the ear. The results can be explained as follows: whilst the young ear was still fully enclosed within the leaf sheaths, with minimal transpirational water flux, B transport into the ear is dependent on the long-distance B transport in the xylem that in turn is driven by leaf transpiration. The transport of B into the ear followed xylem – to – phloem transfers of B taken up by the roots [35]. Shelp et al. [36] similarly concluded that B supply to the head of broccoli depended on xylem – to – phloem transfers. Huang et al. [35] suggested that transfer cells are the likely site for xylem – to – phloem transfer. It possibly involves homologous channels to NIP3;1 found in the nodes of rice [34]. If so, the presence and regulation of B transporters in transfer cells warrants further research in a wider range of plant species. Chaterjee et al. [37] showed the B efflux transporter, Rotten Ear, had strongest expression in the tassel and ear of maize and this transporter was critical for the meristematic growth and cell wall development in those plant parts.

Boron is unique among the essential plant nutrients in that its mobility in the phloem varies among species [38]. Three categories of plants can be recognised according to the phloem mobility of B; species in which B is freely mobile in the phloem due to B-complexing compounds in the phloem, notably sugar alcohols such as mannitol and sorbitol. The free mobility of B in the phloem ensures that B can be retranslocated within the plant especially under deficient supply. However, in most plants B is immobile in the phloem and growing tissues rely substantially on B supplied through the xylem or by xylem – to – phloem transfer [39]. In the majority of plant species where B is immobile in the phloem, interruption of external B supply causes sudden and potentially severe effects on vegetative growth or yield. A third group of plants show an intermediate level of B mobility in the phloem (broccoli – [36]; peanut – [40]; oilseed rape - [41]; various tree species – [42]) but the mechanism is not clear. Stangoulis et al. [43] suggested that B complexes with sucrose may facilitate a degree of phloem mobility but not as much as the sugar alcohols because the B-sucrose complex is weaker. Lehto et al. [42] found variable degrees of B retranslocation among a range of tree species that produce a range of sugar alcohols but could not attribute the variation to the presence or absence, the type or the level of sugar alcohols produced.

Wheat sterility has been attributed to a temporary interruption in B supply to the ear during the period of young microspore development [29]. Low vapour pressure deficit during this period is considered to be an environmental condition that interrupts B flux through the plant and suppresses B uptake into the anthers. Based on the findings of Huang et al. [35], only 3-5 days interruption to B supply would be sufficient to substantially increase pollen sterility in wheat. In woody tree species, dry periods that interrupt B supply can cause wood deformities that make the tree worthless as timber. Presumably, the deformed wood suffered from damage to cell walls during cell expansion. In Figure 5, sunflower leaves in the upper and lower canopy were free of B deficiency symptoms while the mid canopy leaves that formed during a period of drought and restricted B uptake, showed classical B deficiency symptoms (P. Blamey personal communication).

Factors controlling B long distance and short distance transport to zones of expanding cells are not well understood [4]. Interruptions to B supply, or restricted supply of B to these tissues, whether they be in root or shoot (vegetative or reproductive) meristematic regions is likely to induce deficiency. However, in woody plants, B reserves may buffer the growing tissues from restrictions in B uptake [44]. In plant species that are able to freely re-mobilise B as B complexes in the phloem, the meristematic growth is also buffered from interruption of external B supply. Brown et al. [45] for example showed that wild type tobacco suffered B deficiency within 12 hours of transfer from B-adequate solution to minus B solution. By contrast, transformed tobacco containing the gene for sorboitol formation was able to grow normally with no root B supply provided B was applied to leaves. The capacity to produce sorbitol allowed transgenic tobacco to retranslocate B from leaves to the flowers and maintain adequate supply for the flowers to fertilise normally and produce seed.

**Figure 5.** Sunflower showing B deficiency symptoms in mid-canopy leaves that formed during a period of drought and restricted B uptake compared to upper and lower canopy leaves that are free of B deficiency symptoms. Photo credit: P Blamey.

In other cases, the greater tolerance to B deficiency in reproductive plant parts appears to be related not to phloem mobility but to xylem – to – phloem transfer. When exposed to 5 days of low external B (0.1 uM), wheat *cv.* Fang was able to maintain B concentrations in ears at 7 mg B/kg and experienced no change in pollen viability subsequently [46]. By contrast, the same period of low external B supply decreased pollen sterility to 53 % in wheat *cv.* SW41 while the ear B concentration dropped to 3.8 mg B/kg. The extra B in the ear of cv. Fang was attributable to $^{10}$B isotope taken up by roots during the period of low external B supply, rather than the retranslocation of $^{11}$B that had been supplied earlier. Hence it was concluded that *cv*. Fang had greater ability to maintain B supply to the ear during periods of interrupted B supply, and avoid pollen sterility, due to xylem – to – phloem tranfers of concurrent B uptake by roots rather than by retranslocation of previously absorbed B. Further research in B efficient wheat cultivars should examine the expression of B transporters and channels that might facilitate the uploading of B from the xylem into the phloem, possibly through transfer cells in the upper stem nodes.

## 5. Environmental factors affecting B distribution

Several recent investigations suggest that a number of environmental factors induce B deficiency in expanding tissues and are associated with reduced B concentrations in these tissues. Factors include dry soils [47], high light [48], high canopy humidity [35, 49] and low root temperature [50-52]. Some of the environmental effects directly alter B uptake such as dry soils [47]. Others alter demand for B, while others indirectly cause B deficiency by changing the demand for B, or the partitioning of B within the plant.

Huang et al. [48] showed that high light intensity increased the external B requirements for sunflower due to two influences. Firstly, it increased overall B demand in the shoot due to the stimulation of growth. Stimulation of growth will tend to dilute plant B and hence may induce B deficiency if external supply is marginal. In addition, more B was preferentially partitioned to the older leaves presumably because they transpired more water under high light than the young emerging leaves that rely more on xylem – to – phloem transfers to maintain adequate B supply. Similarly Ye et al. [52] concluded that root zone temperature (RZT) above the critical threshold for chilling injury in oilseed rape can alter the incidence of B deficiency by altering shoot–root ratio and hence the balance between shoot B demand and B uptake. In the study by Ye et al. [51], lowering RZT from 20 to 10 °C increased the B concentration in the youngest open leaf in part by decreasing shoot-to-root ratio and in part by increasing the B partitioning to the young leaf. This was attributed to lower water flux to old leaves under 10 °C RZT which together with a decreased demand for B in the young leaf also ensured a continued adequate B supply to those growing leaves. Furthermore, Eichert and Goldbach [49] reported that the mobility of B in the phloem of *Ricinus communis* varied with change in the relative humidity in the shoot canopy. Hence environmental factors alter the distribution of B in shoots by changing B uptake, B demand and B partitioning into growing plant parts where the highest demand for B exists. However, further research is needed to understand how these environmental factors affecting B and water uptake and distribution can be integrated to predict impacts on B deficiency in crops.

## 6. Implications for B fertiliser management

The mobility of B in the phloem has a major bearing on B fertiliser management for a particular crop species. If B is immobile in the phloem, which accounts for most plant species, soil-applied B fertilizers are effective only while soluble and present at sufficient concentrations in the soil solution for adequate plant B uptake. However, the B deposited within the cells of a plant part B cannot be remobilized if B is immobile or only slightly mobile in the phloem. Leaching of B fertiliser may cause soil solution B levels during the growing season to drop below the concentrations required for adequate uptake. In these circumstances the B absorbed earlier by the plant is not available to be remobilized to maintain new growth. Slow release forms of B fertilizer can maintain an adequate supply to the crop for a longer period under leaching conditions [53]. Dry soil conditions in topsoil have been shown to depress B uptake due to restricted B uptake even through the amounts of extractable B may still be sufficient [47].

Foliar B fertilizers can be applied to correct B deficiencies that appear during the growing season [54]. However, B foliar fertilisers are effective only on the tissues sprayed and have no ability to provide sufficient B for subsequent growth of species in which B is immobile in the phloem. By contrast, in species such as almond, foliar spaying of B to leaves in the autumn can be stored in the stem and buds, and remobilised to support new leaf and flower growth in the spring when the demand for B for new growth may outstrip the capacity of roots to absorb B [55].

Soil applications of B are effective in most circumstances, except when high rates of B leaching remove B from the root zone, or dry soil conditions restrict root access to fertiliser B. Species with phloem B mobility are more resistant to short term B deficiency than those without since B stored in old leaves or stems can be remobilized to buffer the decline in root uptake. Temporary B deficiency is difficult to diagnose by plant analysis because the circumstances that lead to a deficiency may have already passed by the time the leaf sample is collected and analysed [56].

Evidence continues to accumulate for a beneficial effect of B foliar applications on expanding tissues, even when plant analysis reveal leaf B concentrations well above the levels required to avoid B deficiency for leaf growth itself [57].

## Acknowledgements

This manuscript was based on a paper presented at AgroBor 2016, the International Symposium on Boron in Agriculture, held at Ankara, 15-17 November 2016. I gratefully acknowledge support of BOREN (The National Boron Research Institute) to attend the conference.

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