Viewpoints

Boron: the essential element for vascular plants that never was

Summary

Although a requirement for boron is a well-established feature of vascular plants, its designation, for almost a century, as essential is challenged and, instead, the proposal is made that it has never been so as conventionally defined. This is because an alternative interpretation of published evidence negates its compliance with one of the criteria for essentiality, that its effects are direct. The alternative, here postulated, is that boron is, and always has been, potentially toxic, a feature which, for normal growth, development and reproduction, needed to be nullified. This was enabled by exploitation of boron's ability to be chemically bound to compounds with *cis*-hydroxyl groups. Although particular cell wall carbohydrate polymers, glycoproteins and membrane glycolipids are among candidates for this role, it is here proposed that soluble phenolic metabolites of, or related to, the components of the pathway of lignin biosynthesis, themselves potentially toxic, are primarily used by vascular plants. When metabolic circumstances allow these phenolics to accumulate endogenously in the cytoplasm, their own inherent toxicity is also alleviated, partially at least, by formation of complexes with boron. This chemical reciprocity, enhanced by physical sequestration of the complexes in vacuoles and/or apoplast, thus achieves, in a flexible but indirect manner, a minimization of the inherent toxicities of both boron and relevant phenolics. In these ways, the multifarious outcomes of impairments, natural or experimental, to this interplay are responsible for the lack of consensus to explain the diverse effects observed in the many searches for boron's primary metabolic role, here considered to be nonexistent. In particular, since a toxic element cannot have 'deficiency symptoms', those previously so-called are postulated to be largely due to the expressed toxicity of phenylpropanoids. A principal requirement for the otherwise toxic boron is to nullify, by means of its indirect chemical and physical sequestration, such expression. In these ways, it is therefore neither an essential nor a beneficial element as currently strictly defined.

Background

> 'As we examine the role of micronutrients . . . we enter murky waters when we consider the functions of boron'
>
> (Hull, 2002)

Arnon & Stout (1939) listed three criteria that needed to be fulfilled for an element to be declared 'essential' for vascular plants. These, still currently observed, are, in short, failure to complete lifecycle in its absence, cannot be substituted by another element, and action direct. A fourth, that the first three are applicable to all vascular plants, may be added. Warington (1923), had already included boron as one such element. In the subsequent 95 years, her claim that there is a positive requirement for boron has been repeatedly made in the numerous reviews of the extensive literature concerning boron's chemical and biological relevance to plants in both purely scientific and applied (agri-, arbori- and horti-cultural) aspects. However, there is no consensus about its primary role, another point repeatedly made. This repetition is well illustrated in the introductory section of the 1998 multi-reference review by Blevins & Lukaszewski where 16 earlier reviews are listed. Although the comprehensive review of Goldbach (1997) with *c.* 200 references was not included in their list, probably because it was written contemporaneously, features from it, along with others from Blevins & Lukaszewski (1998) and Camacho-Cristobal *et al.* (2008), particularly relevant to the thesis to be developed, are highlighted later. A later mini-review by Kutschera & Niklas (2017) summarized boron's role as 'multifunctional'. This assessment contrasts with the roles of other essential micronutrients that generally have restricted, specific roles. Despite this contrast, there has been no challenge to boron's presumed essentiality since researchers concerned with its role have accepted that it has a positive, direct, albeit elusive, one and so satisfies all criteria for essentiality. That no primary role has been agreed despite the long history of research surely indicates that it does not have one.

The ongoing acceptance of boron's essentiality is, therefore, challenged here by the deliberately provocative proposal that it is not essential in the conventional sense because it is always toxic and so cannot have a primary role. This viewpoint is taken to stimulate discussion as the century of research, due five years hence, on this unresolved subject approaches. It is a theoretical proposal for the metabolic mechanism by which the postulated toxicity of boron is not only overcome but also put to good purpose in particular circumstances.

The voluminous publications concerning boron and vascular plants broadly divide into two categories, those that extend the range of species showing responses to boron similar to features already established, and those that review suggestions for possible roles for these responses. This article does not purport to be a comprehensive review but one that principally takes evidence, interpreted to support the proposal, from the latter category. With regard to the practicalities of commercial applications of boron, the article by Hull (2002), from which its opening sentence is quoted earlier, is a good source of scientific information for the layman. In particular, his Table 2 summarizes the various roles that have been proposed for boron.

For brevity, and to avoid repetition with these reviews, references to the observational and experimental details that have given rise to accepted, noncontroversial, conclusions about effects of boron are therefore restricted. Also for brevity, 'boron' is used, as the context demands, to mean the element, boric acid, the borate anion, its organic complexes or combinations of these.

Hypothesis

The alternative viewpoint that boron is toxic and so not essential in the strictly defined sense is based on three premises.

The first, maintained throughout this article, is that when vascular plants initially evolved, boron was a globally present element at varied concentrations in available rooting media but one that was, and has remained, phyto-toxic and potentially lethal.

The second premise is that, to ensure the necessary mitigation of this toxicity that has allowed the development and spread of vascular plants, natural selection has brought about the evolution of a constitutive biochemical mechanism that maintains an appropriate homeostatic balance between the quantities of boron absorbed and the amounts of neutralizing agents synthesized. Owing to the suggested constitutive nature of these reactions, it is also proposed that, when boron is naturally absent, present in low concentrations or experimentally withheld, the continuously synthesized free neutralizing agents would not only accumulate when not required for other purposes but also themselves exert toxic effects.

The third premise is that the required detoxifying neutralization was, and is, achieved by chemical sequestration of absorbed boron as readily formed complexes with particular compounds containing *cis*-hydroxyl groups together with their physical sequestration away from sites of normal cytoplasmic metabolism, so allowing uninhibited, normal growth and development.

Evidence and speculation

With regard to the first premise, the concentration-dependency of boron's positive and negative effects on species and varieties is well documented, especially by Goldbach (1997). The alternative viewpoint envisages that even effects noted at low external concentrations of boron will have necessitated the mitigation of its toxicity as required by the other premises. Also and in particular, a corollary to the designation of boron as always toxic to vascular plants is that it cannot have 'deficiency symptoms'. The myriad of differences between vascular plants, when grown ± boron, are very well recorded and discussed, again in particular by Goldbach (1997) (see his sections 2.2, 2.3 and extensive Table 1) and are effectively catalogued in the other reviews cited earlier. They thus need assessment from this altered perspective. This is done later for one general and four specific phenomena, chosen because, although the latter may appear at first sight to be unrelated, they are shown collectively to provide evidence in favour of the hypothesis. These are the relevant biochemical activities of boron involved with (1) growth and development of plants in general and, more specifically, with (2) lignification, (3) responses of plants to wounding, (4) adventitious rooting of cuttings and (5) pollination.

With regard to the second premise, Blevins & Lukaszewski (1998) recalled that, Warington's article in 1923 first proposed boron to be an essential element, she also recorded that its supply required to fulfil its then considered functions needed to be continuous. This implies that the metabolic pathways, here deemed necessary to cope with incoming boron's toxicity, are always active, that is, they are constitutive.

Among the categories of the most probable neutralizing agents required by the third premise, four may be delimited. Two, glycolipids in membranes and glycoproteins in general, are not explored further here since the much better studied polymeric cell wall carbohydrates and phenylpropanoids are considered to be more likely candidates. Of the former, much attention has focused on rhamnogalacturonan-II, a pectic polymer which, without doubt, is cross-linked by boron, one attribute among the many claimed to be a primary role for the element (Matoh, 1997; O'Neill *et al.*, 2004; Chormova & Fry, 2015). However, unless such cross-linking facilitates electric signalling (see W-G. Choi *et al.*, 2017 in relation to this topic), the responses are considered here to be more likely to occur in the cytoplasm rather than cell walls. Of particular note favouring this initial location for these neutralizing biochemical processes, when studied in either whole plants or in their experimentally isolated organs/tissues, both to withdrawal of boron from those previously adequately supplied and to supply of the element to those previously deprived, is the rapidity by which the responses occur, an aspect regularly commented upon in the cited reviews. Thus, attention in this article is largely focused on the involvement of soluble phenylpropanoids as neutralizing agents rather than insoluble carbohydrate polymers. This viewpoint therefore requires an explanation of how control is achieved over the adverse effects of the simultaneous toxicity of both boron and relevant phenylpropanoids. This is outlined later after boron's metabolic involvements in the five disparate areas chosen for comment have been addressed.

1. Growth and development of plants in general

The principal differences between plants grown ± boron, covered in the reviews listed earlier and in the comments also made earlier concerning the first premise, are not re-catalogued here. Instead, the common underlying metabolic events bringing about the many differences are explored.

That endogenous phenolic acids with *cis*-hydroxyl groups (such as caffeic, chlorogenic, hydroxyferulic, quinic and dehydroquinic acids and derivatives from them) accumulate when boron is in short supply with adverse metabolic effects, reflected in disturbed development, has been known for over 60 years. (See early references relating to caffeic and chlorogenic acids in Table 1 and section 2.4 of Goldbach (1997) and Table 2 of Lewis (1980a).) The latent toxicity of these phenolics had even earlier been established by A. D. M. Glass and co-workers (see Glass & Dunlop, 1974). They and others (e.g. Batish *et al.*, 2008) showed that exogenous supply of phenolic acids could mimic the toxicity brought about by their endogenous accumulation. These wide ranging observations provide sound evidence for the generalization that low endogenous concentrations of boron are correlated with an enhanced presence of potentially toxic phenolics. Supporting evidence for their potential and actual toxicity comes from studies of allelopathy, unrelated to those involving boron. This work, particularly that in the laboratory of U. Blum, has firmly established their involvement as toxic agents in allelopathic interactions (see Blum & Gerig, 2005; Blum, 2011).

To ensure normal metabolism, both sources of toxicity clearly need to be nullified or, at least, minimized. That due to boron's inherent, concentration-dependent toxicity is wholly or largely (since other compounds such as rhamnogalacturonan-II may also act in a minor way) achieved by combination of the offending element with commensurate, stoichiometric amounts of appropriate phenolics; that due to phenolics is managed in a reciprocal manner, i.e. by combination with available boron. In addition to this chemical mitigation, physical sequestration of free or complexed boron in vacuoles and/or apoplast also enhances the maintenance of the uninhibited cytoplasmic metabolism required for normal growth and development. Such compartmentation, mentioned in Lewis (1980b), was proposed by Rozema *et al.* (1992) to account for the tolerance of halophytes to the high concentrations of boron they naturally encounter. Here, this proposal is extended to all vascular plants in all soils and artificial rooting media. Such sequestration could also then potentially act as an endogenous store of unreactive boron, which can be called on rapidly to assist the nullification of excess constitutive cytoplasmic synthesis of toxic phenolics. The available evidence therefore satisfies the requirements of the second and third premises.

Much attention has recently been given to the molecular biology of the transporters involved with the uptake, export and internal distribution among discrete cellular and cell wall compartments of boron. Cardinal research and review articles include Hayes & Reid (2004), Reid (2007, 2014), Takano *et al.* (2008) and Miwa & Fujiwara (2010). Julkowska (2018) has provided a summary. The content of these papers, although clearly relevant to the mechanism of physical sequestration, are not considered further here since they do not contribute significantly to the present discussion of the essentiality of the element. In passing, it is noted that transporters for a toxic element are not unique to boron. Those of another, arsenic, are also well documented (Farooq *et al.*, 2016).

2. Lignification

Synthesis of lignin is initiated by the conversion of phenylalanine to cinnamate, catalysed by the enzyme phenylalanine-ammonia-lyase, and continued by a series of methylations and hydroxylations which result in the formation of the various phenylpropanoid precursors of the complex lignin polymers (Weng & Chapple, 2010). These are elaborated in vascular plants into the supporting and water-conducting tissue, xylem (Raven, 1977, 2018). Lewis (1980a) speculated, in relation to the origin of land plants, that boron was intimately involved with this synthesis and differentiation, a topic also briefly alluded to by Lovatt (1985), Josten & Kutschera (1999) and Kutschera & Niklas (2017). Although the metabolic interactions between boron and phenolic acids resulting in the homeostatic outcome proposed later must have had their beginnings around the time of these events, this evolutionary aspect is not pursued here other than to withdraw the specific suggestion in Lewis (1980a) that boron had a positive primary role in the methylation and hydroxylation steps in these metabolic pathways. The intermediates in the pathways (and, doubtless, other 'secondary' phenolic metabolites; Hartmann, 2007) nevertheless have had, and currently continue to have, important interactions with boron (see later).

3. Responses of plants to wounding

Plants are regularly naturally damaged by both biotic (grazing, microbial infection, etc.) and abiotic (wind, drought, etc.) means. Again, a frequently recorded characteristic response to such damage has been the accumulation of particular phenolic acids and other phenylpropanoids, including phytoalexins. For earlier references, see Lewis (1980b) and the reviews cited earlier in this Viewpoint. Although primarily concerned with bacterial infections by *Agrobacterium* and *Rhizobium*, a more recent review by Bhattycharya *et al.* (1997) also provides an extensive catalogue and analysis of the phenolics produced by plants in response to sundry stresses as do Y-J. Choi *et al.* (2005), specifically for lettuce (*Lactuca sativa*) in a paper which crossed the boundary between the two characteristic types of publication about boron and plants delimited earlier in the Background section. Here, as a prelude to the next section, it is sufficient simply to note, along with Dixon & Paiva (1995), that the natural, stress-induced synthesis of a multiplicity of phenolics is a common feature in plants. As this natural feature is likely to be involved with boron, the following section concerns the deliberate wounding involved with propagation using cuttings, a process of substantial commercial importance in agriculture, horticulture and forestry.

4. Adventitious rooting of cuttings

Metabolic processes involving adventitious rooting of cuttings and supply of boron have been extensively investigated. As the preparation of the cuttings is a wounding action, what has already been said in relation to phenolics in the previous section on wounding, is intimately relevant. Also, highly apposite is the involvement of plant hormones, an aspect not elaborated here as it is not directly important to the theme of this viewpoint (but see Eggert & von Wiren, 2017). Of especial relevance are the observations of B. C. Jarvis *et al.* in a series of papers on various features concerning adventitious rooting published in the 1970s and 1980s and described in Goldbach (1997) as 'thorough'. Of special relevance is the report in Middleton *et al.* (1978), a paper described as 'classic' by Kutschera & Niklas (2017), that fresh cuttings from healthy seedlings of mung bean (*Phaseolus aureus*/ syn. *Vigna radiata)* do not require boron to take root but that aged ones do. This particular effect is explicable from this Viewpoint's perspective as follows. When cuttings are taken from healthy plants, all free phenolics would be present at a nontoxic concentration but, during the ageing period, they would accumulate as a response to wounding, thereby generating a requirement for boron to neutralize their adverse effects. Boron's requirement for the rooting of cuttings of sunflower (*Helianthus annuus*) reported by Josten &

Kutschera (1999) may be explained in a similar manner. Detailed analysis of this sequence of metabolic events for individual species (or varieties) of commercial importance could improve methods for their large-scale propagation, both quantitatively and qualitatively. Also in line to contribute to such improvements are molecular aspects of the process, now being addressed in *Petunia rigida*, a model plant for such investigations (Ahkami *et al.*, 2009).

5. Pollination

Two aspects of the involvement of boron with pollination were noted earlier and have subsequently been confirmed and well recorded in the reviews cited earlier. The first is that stigmas, because they are transpirational termini like apical meristems (Lovatt, 1985), become boron-rich tissues; the second is that boron is required for the *in vitro* germination and tube growth of pollen (Stanley & Loewus, 1964; Stanley, 1971) (see also the cited reviews, especially Blevins & Lukaszewski, 1998). However, there appears to have been few reported experimental studies of its function and metabolism in these tissues and cells. In the light of conclusions made earlier for its involvements in the other aspects chosen for comment, it is probable, despite the limited available evidence, that boron's potential damage in stigmas and germinating pollen is offset by binding to phenolics. For example, Chauhan *et al.* (2004) studied seasonal seed set in the ornamental but invasive shrub, *Tecoma stans*, and reported that infertility in the summer months (May–July) was correlated with raised amounts of phenolics and lowered boron in stigmas. Caffeic acid inhibited *in vitro* germination of its pollen. Wang *et al.* (2003) also recorded an increase in unidentified phenolics in pollen tubes of the gymnosperm, *Picea meyeri*, when germinating in boron-deficient, compared with boron-sufficient, media. More generally in pollen tube growth in the fertilization process is the involvement of the glucan, callose. Unlike the slow synthesis of pectic polysaccharides relative to that of phenolics mentioned earlier, the formation of callose during the exceptionally fast growth of pollen tubes is rapid. Although callose does not contain *cis*-hydroxyls, binding of boron is possible via appropriate juxtaposition of its chains (Lewis, 1980b). Such between-chain binding would thus contribute to nullification of boron's potential toxicity during fertilization. More information on the involvement of boron in the sexual reproduction of plants is still required to fulfil the comment of Lohnis in 1937 (quoted by Blevins & Lukaszewski, 1998) that 'it is quite conceivable that it will be the study of pollen that may elucidate the very fundamental part boron plays in the biochemical processes'.

Conclusions

It is clear from the recorded or inferred evidence in the earlier five, and probably other, vignettes, that a consistent theme is an interplay between phenolics and boron, an element here speculatively deemed to be toxic. It is concluded that its adverse effects are mitigated by its chemical (as organic complexes) and physical (into vacuoles/apoplast) sequestration. Although some chemical binding occurs with pectic polysaccharides, this is not here regarded as a controlling effect compared with that due to phenolics, the constitutive synthesis of which is so important for the elaboration of lignin, development of xylem and the colonization of land. Their synthesis did not come about without causing biochemical problems owing to their own ongoing toxicity. The initial overcoming of this second toxicity, from the evidence presented earlier, took advantage of the simultaneous presence and availability in the environment of boron, an otherwise toxic element but with chemistry suitable to be engaged in minimizing the adverse properties of phenolics. Because such involvement, still required, is an indirect effect, it disqualifies the element as 'essential' because it does not fulfil the third criterion for essentiality in Arnon & Stout's (1939) list. (Also, boron's adherence to the fourth criterion for essentiality mentioned earlier means neither does it qualify as a 'beneficial' element.) Nevertheless, boron, despite its toxicity, is still required for normal growth and development of vascular plants. A corollary to the conclusion that boron is not essential is that much previous research setting out to analyse its primary role effectively became studies of abnormal metabolism caused by the adverse inhibitory effects of miscellaneous phenylpropanoids present in excess of the binding capacity of endogenous boron. Its toxicity is consequently also brought about indirectly via the accumulation of one or more constitutively synthesized phenolics. In this manner, inadequate provision of binding agents allows boron's toxicity to be expressed.

Future analysis of the interplay of phenolics with boron will ideally require both qualitative identification and quantitative determination of the phenolics and boron species involved. Such knowledge potentially will then guide genetic or other manipulation of their collective or individual loads with predictable and, therefore testable, outcomes. For example, raising endogenous concentrations of phenolics, for example by applying limited stress, will increase tolerance to high soil boron; a lowering will decrease it. Also, it can be predicted that excess phenolics will herald a return of what were previously called 'deficiency symptoms'. Where previous experiments have been proposed to signal primary roles, their data need to be re-examined or repeated to check that effects are not due to accumulation of phenolics. Future experiments must therefore include appropriate controls to do this. The ability to customize tolerance to boron potentially allows the development of species and varieties for particular soils of varied boron loads. Also, the optimal conditions for formation of adventitious roots noted earlier are determinable, so rendering outcomes testable when extended to further species and varieties. It would thus appear that all previous proposals for its primary role would need to have had any effects attributable to phenolics eliminated before others were added. These conclusions also imply that the adverse outcomes of the two sources of toxicity could well have resulted in confusion and be responsible for the lack of consensus about boron's (nonexistent) primary role.

Those readers who still are ready to search for a conventional primary role, their future experiments must include appropriate controls to eliminate the involvement of phenolics.

Two situations where effects of phenolics, not involving boron, were mentioned earlier. These were their accumulation consequent to various stresses and their being active components during allelopathic interactions. Should effects of boron in these situations be tested in future, it can be predicted that, via the complexing of phenolics, both stress and adverse allelopathic effects would be lessened, another testable proposal. Also it is possible that manipulation, via varied supply of boron, of the kind and amounts of phenolics generated by different stresses could be exploited in biofarming/biopharming to produce desirable compounds. Also, future optimization of the amount and timing of supply of boron to stimulate the development of adventitious roots, in the manner noted earlier, also would be predictable and testable in line with the dual toxicity hypothesis.

One anonymous referee made the valid comment that the situation in the fern gametophyte, the nonvascularized stage of the life cycle of a vascular plant, requires attention. The hypothesis would conclude that, unless phenolics had other roles besides lignin biosynthesis, boron would be toxic at all concentrations and not be able to be chemically sequestered. This seems unlikely and too ecologically restrictive but needs investigation.

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