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McGrath, S. P. 2020. Arguments surrounding the essentiality of boron to vascular plants. *New Phytologist.* 226 (5), pp. 1225-1227.

Commentary

Arguments surrounding the essentiality of boron to vascular plants

David Lewis's (2019) original Viewpoint article on this subject was intentionally provocatively titled 'Boron – the essential element that never was'. The intention was to grab our attention, and has quickly drawn two Letters from boronologists and two responses from David Lewis, that are published as a cluster of four in this issue of *New Phytologist*.

'This has been a useful scientific debate which I feel is an excellent function of the journal.'

The element boron (B; Fig. 1) was discovered in Paris by Louis-Josef Gay-Lussac and Louis-Jacques Thénard in 1808, and independently by Sir Humphry Davy in London. The name is derived from the Arabic 'buraq', which was the name for borax. It is classified as a semi metal or metalloid (with some chemical similarities to silicon (Si), germanium (Ge) and arsenic (As)). Over a hundred years later, Katherine Warrington showed that B was essential for certain plants (Warrington, 1923). Lewis's Viewpoint reminds us of the three criteria that have been used to define whether an element is essential or not (Arnon & Stout, 1939). These are: (1) that a plant cannot complete its life cycle in the absence of the element; (2) the element cannot be substituted by another element; and (3) the element has a direct function in plant metabolism. Some 17 elements are now considered essential (Fig. 2) and a further four are beneficial at least to some plant species. As 2019 was the 150th anniversary of the Mendeleev periodic table, perhaps this is a very appropriate time for the community to review which elements are important for plant growth, and at the same time to improve our understanding of their exact status.

Boron is generally regarded as essential, but Lewis (2019) questions this, even though poor growth and visible symptoms of deficiency can be readily seen in some plant species (Fig. 3). Crops and forages susceptible to B deficiency include legumes, brassicas, sugar beet, celery and sunflowers and under low B conditions supply of B in fertiliser is important for their production. His interesting Viewpoint basically questions whether B has a direct function in plant metabolism, arguing instead that its effects on growth may be indirect. Instead, he postulates that B is potentially toxic, and that it binds other potentially toxic compounds, in particular soluble phenolic metabolites. His proposition is that B deficiency symptoms (Fig. 3) are in fact due to the toxicity of phenylpropanoids. He argues in this case that B has no direct function of its own, but only prevents the toxicity of those compounds by their indirect chemical and physical sequestration with B.

The Letter by Augustín González-Fontes (2020; pp. 1228–1230) in this issue of *New Phytologist*, largely re-iterates what is known about the effects of B and its role in cell wall structure, B transporters and the toxicity of plant phenolics. He gives a lot of emphasis to the fact that inducible high affinity transporters for B exist, which is an important point that Lewis dismissed in his published Viewpoint by invoking the existence of As transporters. However, the latter appears to be a classic case of accidental uptake by transporters that actually evolved to take up the chemically similar molecule silicic acid (beneficial element Si) but also transport arsenious acid, H_3AsO_3, particularly strongly in the case of rice grown in flooded conditions (Ma *et al.*, 2008; Zhao *et al.*, 2010). Incidentally, the other predominant As species prevalent under aerobic conditions, arsenic acid (H_3AsO_4), is probably taken up by phosphate transporters. Evidence for specific B transporters exists.

In his response to González-Fontes, Lewis's Letter (2020a; p. 1231) in this issue of *New Phytologist*, starts out by emphasizing that his original Viewpoint was largely theoretical. The argument is over whether the effects of B are direct or indirect, that is whether it fits criterion (3) above. The original Viewpoint (Lewis, 2019) and this Letter state that this is really not proven, and more research is needed. I must say that at this point I re-read the section on B in Marschner's book (Marschner, 2012). On balance, the reader is left with the impression that many of the effects of B seem rather indirect. One particularly telling quote is that 'The role of B in plant nutrition is still the least understood of all the nutrients and what is known of B requirement arises mainly from studies in which B was withheld or resupplied after deficiency' (Marschner, 2012). Boron has no recognized role as a functional component of any enzyme and there is no evidence that it affects the activity of any enzyme. One can begin to see why Lewis came up with the hypothesis that the effects of B are indirect. His Letter will stimulate further discussion and future experimentation that will surely clarify the role of B.

Lewis (2020a) also mentions that if there is evidence of both direct and indirect effects of B, that some rewording of the definition of essentiality may be needed. This can be confusing for students and professionals alike! The original Viewpoint article (Lewis, 2019) states that B 'is therefore neither an essential nor a

This article is a Commentary on González-Fontes (**226**: 1228–1230), Lewis (2020a, **226**: 1231), Wimmer *et al.* (**226**: 1232–1237), Lewis (2020b, **226**: 1238–1239)

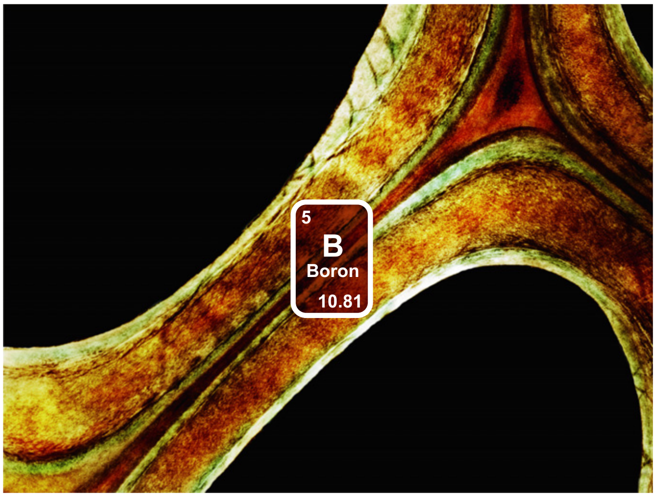

Fig. 1 The atomic number, chemical symbol and standard atomic weight of boron (B) shown in a plant cell wall, where it plays a role in biosynthesis and structure of cell walls. Coloured transmission electron micrograph (TEM) of cell walls in wood of the Canadian yew (*Taxus canadensis*). The outermost layer of a cell wall, the middle lamella (red), is shared between adjacent cells. Inside this is the primary cell wall (pale green) of cellulose fibrils in a matrix of pectin. Woody plant tissues also have a secondary cell wall (orange) of cellulose and lignin. Inside the secondary cell wall and next to the cell contents (black) is the plasma membrane. Magnification: ×63 000 when printed 10 cm wide. Image credit: SCIENCE SOURCE/SCIENCE PHOTO LIBRARY.

beneficial element as currently strictly defined'. Readers may be confused, and I feel discussion is needed about the difference between these, as a contribution to both plant science and crop husbandry.

A strong squad of boronologists then responded in detail to Lewis's Viewpoint (2019) in quick order: Wimmer *et al.* (2020; pp. 1232–1237) in this issue of *New Phytologist*. Their Letter is well reasoned, and it provides an excellent review of the evidence for the essentiality of B to plants. It is well organized into discrete sections that address each of the arguments in turn, and is also well referenced with all the key papers in the area. I find it an excellent contribution to the debate begun by the largely theoretical paper by Lewis (2019), and applaud the authors for putting together this valuable contribution to the arguments. They point out that B fulfils the first two criteria for essentiality and that it is the function in cell wall metabolism that is unambiguous and therefore fulfils

Fig. 3 Boron (B) deficiency (left) in *Brassica napus*. (Photograph credit: R. M. Norton, Image ID: IPNI2015RNO03-1274, copyright International Plant Nutrition Institute 2020).

criterion (3). Discovery of its role in the form of a borate diester cross-linking rhamnogalacturonan-II (RG-II) molecules, this pectic polysaccharide was a major advance in understanding its structure and function, in all vascular plants (O'Neill *et al.*, 2004). Wimmer *et al.* also point out the at least one bryophyte lacks RG-II and has high levels of free B in its cell walls without toxicity, contradicting Lewis' toxicity hypothesis. In particular, I find the comments about the 25-fold surplus of phenolic compounds in plants grown under sufficient B supply very persuasive. Also very telling was the 10- to 15-fold lower requirement in graminaceous plants compared to dicots, even though there is no evidence for much lower phenol concentrations in those plants. This also explains why grasses respond less to B fertilisers when grown on the same soils as the more sensitive dicot species listed above. Wimmer *et al.* discuss the available information on the amounts and timing of production of phenols in plants and usefully suggest ways of testing the toxicity quenching hypothesis of Lewis. In addition, their Letter usefully points out where information is still missing and suggests some further research to strengthen the evidence for the essentiality of B.

David Lewis's response (2020b; pp. 1238–1239) in this issue of *New Phytologist* accepts most, if not all, of the very good arguments by Wimmer *et al.* As David Lewis points out, Wimmer *et al.* and Gonzáles-Fontes in the previous article have not commented on the

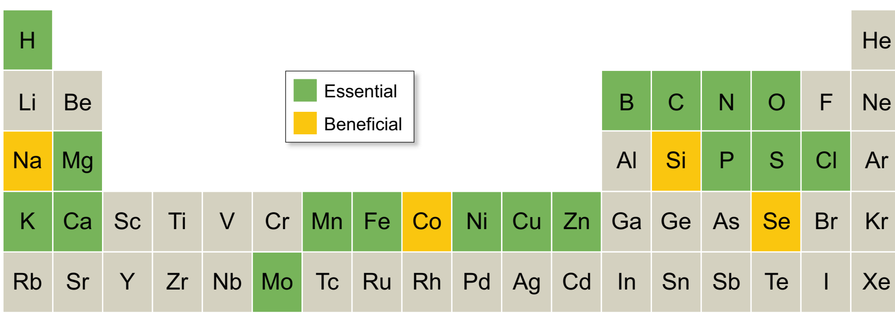

Fig. 2 Essential and beneficial elements for higher plants (only the first five rows of the periodic table are shown).

effects that B might have on allelopathic interactions between species. This is another interesting suggestion by Lewis that may stimulate further comment and debate by others who are more involved in research on allelopathy, and encourage further debate.

This has been a useful scientific debate which I feel is an excellent function of the journal. I feel that the views expressed in the Letters and responses serve to encourage not only scientific debate, but also stimulate the community to think and perform suitable experiments that test the hypothesis of Lewis – the scientific method. This is the way that science should work, and one can see from reading their contributions that this debate has been conducted with appreciation and good humour on all sides.

In finishing, I can reveal a kind of vested interest. Katherine Warrington, from Harpenden, worked in my Institute when she published the work showing that B was essential for vascular plants, and I like to think that I was instrumental in her name being used to name a new secondary school in the local area – Katherine Warrington School – which opened in September 2019 (http://kwschool.co.uk/). I hope that her name and achievements make the pupils look at plant nutrition and thus come to understand it more and stimulate our profession, and indeed these kinds of discussion, in the future.

Acknowledgements

This work was funded by the Biotechnology and Biological Sciences Research Council in the Soil to Nutrition Institute Strategic Project (BBS/E/C/000I0310). The author wishes to thank David Lewis for teaching him about plant science and the late Bernie Jarvis about boron at the University of Sheffield (UK).

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Key words: allelopathy, boron (B), cell wall, essential element, plant metabolism, phenolics, toxicity, vascular plants.