



# What is a plant nutrient? Changing definitions to advance science and innovation in plant nutrition

Patrick H. Brown · Fang-Jie Zhao ·  
Achim Dobermann 

Received: 9 July 2021 / Accepted: 27 September 2021 / Published online: 16 October 2021  
© The Author(s) 2022, corrected publication 2022

**Abstract** Current definitions of essential or beneficial elements for plant growth rely on narrowly defined criteria that do not fully represent a new vision for plant nutrition and compromise fertilizer regulation and practice. A new definition of what is a plant nutrient that is founded in science and relevant in practice has the potential to revitalize innovation and discovery. A proposed new definition might read: *A mineral plant nutrient is an element which is essential or beneficial for plant growth and development or for the quality attributes of the plant or harvested product, of a given plant species, grown in its natural or cultivated environment. A plant nutrient may be considered essential if the life cycle of a diversity of plant species cannot be completed in the absence of the element. A plant nutrient may be considered beneficial if it does not meet the criteria of essentiality, but can be shown to benefit plant growth and development or the quality attributes*

*of a plant or its harvested product.* It includes elements currently identified as essential, elements for which a clear plant metabolic function has been identified, as well as elements that have demonstrated clear benefits to plant productivity, crop quality, resource use efficiency, stress tolerance or pest and disease resistance. We propose an open scientific debate to refine and implement this updated definition of plant nutrients. Other outcomes of this debate could be a more precise definition of the experimental evidence required to classify an element as a plant nutrient, and an independent scientific body to regularly review the list of essential and beneficial nutrients. The debate could also attempt to refine the definition of plant nutrients to better align with nutrients deemed essential for animal and human nutrition, thus following a more holistic 'one nutrition' concept.

---

Responsible Editor: M. Iqbal R. Khan.

---

P. H. Brown  
Department of Plant Science, University of California  
Davis, One Shields Ave, 95616 Davis, CA, USA

F.-J. Zhao  
College of Resources and Environmental Sciences,  
Nanjing Agricultural University, 210095, China Nanjing,  
China

A. Dobermann (✉)  
International Fertilizer Association (IFA), 49 avenue  
d'Iena, 75116 Paris, France  
e-mail: adobermann@fertilizer.org

**Keywords** Plant nutrients · Definition · Essential elements · Beneficial elements

## A new paradigm for plant nutrition

Plant scientists as well as regulatory bodies largely adhere to a rigid definition of *essential mineral elements* (or nutrients) for plants that was originally proposed in 1939 (Arnon and Stout 1939), and has been repeated in standard monographs on plant nutrition ever since. This very narrow definition of essentiality considers an element as a plant nutrient only in the context of the

completion of the lifecycle of the plant. It excludes from consideration many plant nutrients that ‘only’ enhance plant growth, improve the efficiency of utilization of nutrients, water, and other resources, enhance abiotic or biotic stress tolerance, or improve the quality or nutritional value of the harvested product.

In the science, regulation, commercialization and use of fertilizers and other sources of plant nutrients the definition of an ‘essential element’ has considerable importance. Although no universally accepted body exists for regularly reviewing and updating the ‘established list’, for practical purposes 17 elements are commonly classified as ‘essential’ for plant growth, namely carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), sulfur (S), calcium (Ca), magnesium (Mg), chlorine (Cl), boron (B), zinc (Zn), manganese (Mn), iron (Fe), copper (Cu), molybdenum (Mo), and nickel (Ni). Others, such as sodium (Na), silicon (Si), selenium (Se), aluminum (Al), cobalt (Co) or iodine (I), are known to also beneficially impact plant growth, but they are relegated to a legal and practical ‘no man’s land’. In most countries they cannot be legally referred to, marketed or sold as plant nutrients. Historically that has not always been the case. In the 19th century, pioneers of the mineral nutrition of higher plants (e.g. de Saussure, Boussingault, Sprengel, Liebig, Lawes and Gilbert) were primarily interested in improving agricultural growth through mitigating nutrient deficiency (Nortcliff and Gregory 2013). Some elements deemed quite essential by them (e.g. Si, Na) are nowadays mostly in the no-man’s land area because definitions and methodologies changed over time. In contrast, research on essentiality proceeded much faster in animal nutrition. By 1981, 22 mineral elements were classified as essential for animal life, which also led to significant improvements in animal diets and supplements (Suttle 2010).

Science and practice of plant nutrition must refocus on optimizing the full scope of food, socioeconomic, environmental and health objectives necessary to sustain a healthy global population and environment (Scientific Panel on Responsible Plant Nutrition 2020). Many in the global scientific community, as well as agricultural producers, policy makers and industry who are engaged in agriculture, nutrition and environment, have embraced this new vision but may find the science of plant nutrition and its practical implementation constrained by a too narrow definition of a ‘plant nutrient’.

This opinion article is a call for new thinking that begins with updating our understanding of what is a plant nutrient. We propose a new definition for plant nutrients merely as a starting point for further discussion. We focus on the known chemical elements of the periodic table which can be provided to the benefit of crops grown in an agricultural setting, but we also elaborate on possible further expansions of such a debate and definition. We hope that by rethinking the definition of a plant nutrient in the context of the holistic goals of plant nutrition we can encourage a new generation of plant nutrition researchers, spur innovation in public and private sector, and sustainably improve food systems.

### Plant nutrients: a historical perspective

The beneficial effect of adding ash or other forms of minerals to soils to improve plant growth has been known for more than 2000 years, but it was mainly in the 19th century that a broader understanding of the role of different elements arose (Kirkby 2012). Nicolas Théodore de Saussure was perhaps the first to show that developing plants require mineral nutrients, often in very small amounts, insisting that some elements absorbed by plants were indispensable, while others might not be essential (Saussure 1804).

Carl Sprengel, in a series of papers published in the 1820 and 1830s, listed 20 elements that he considered to be plant nutrients (Van der Ploeg et al. 1999). Building on Sprengel’s work, Justus von Liebig erroneously believed that the elemental composition in plants was constant and could thus serve as a measure of nutrient need (Liebig 1840; Macy 1936). Lawes and Gilbert, however, demonstrated that neither the presence nor the concentration of an element in a plant could serve as a reliable indicator for its nutrient needs or as a guide for its fertilizer needs (Lawes and Gilbert 1851; Macy 1936). Nevertheless, by the end of the 19th century, the value of adding certain elements to crop production had been demonstrated and farmers, particularly in Europe, were applying new types of ‘mineral’ fertilizers to their crops (Kirkby 2012). The new plant nutrition findings also spread quickly beyond Europe. For example, from 1882 to 1910, superphosphate was also almost universally adopted by wheat farmers in South Australia (Byerlee 2021).

It became clear that a more precise study of the essentiality of specific elements required new

techniques. Nutrient solution culture, first tried by Boussingault around 1840 and further improved in the 1850 and 1860 s by Sachs and particularly Knop (Knop 1860), allowed for a more precise control of nutrients under experimental conditions, and thus became the principle method of plant nutrition research. Sachs, in his first major book, states that one cannot call a substance a plant nutrient just because it is present in the plant (Sachs 1865). On pages 114–115 he goes on proposing and elaborating two criteria for distinguishing *essential* (“unenthbehrlich”) from *non-essential* (“enthbehrlich, unnöthig”) plant nutrients:

- (i) a structural criterion: the element is an integral component of the chemical formula of plant substances, without which a cell cannot exist (e. g., C, O, H, N, S);
- (ii) a physiological criterion: demonstration that the plant under otherwise good growth conditions cannot complete its vegetation cycle without uptake of any form of the element in question.

He pointed out, however, that testing for the second criterion is experimentally challenging because it is difficult to completely exclude a nutrient from the system (including the seed). Nevertheless, applying the second criterion, he concluded that the elements K, Ca, Mg, Fe and P were also essential, whereas Na and Cl appear to be non-essential. That, we dare say, probably marks the origin of the strict definition that is still in use today.

For a long time, it seemed that the list of essential elements would remain at the 10 already mentioned by Sachs in 1865, but it grew quickly in the 1920 and 1930s, when Mn (1922), B (1923), Zn (1926), Cu (1931) and Mo (1938) were added to it (Kirkby 2012; Hoagland and Arnon 1948). To a large extent this expansion resulted from improvement of analytical methods and refinement of culture techniques, particularly purification of nutrient solutions, as well as widening the research to different plant species that had higher nutrient requirements than others (Hoagland and Arnon 1948). Terms such as *micronutrients* or *trace elements* were coined during that time too, to depict nutrients that were required only in very small amounts in the physiology of the plant. The question arose, which of those were indispensable to growth or not. Motivated by that purpose, Arnon and

Stout (1939) postulated that a plant nutrient can be considered essential only if

- (i) “a deficiency of it makes it impossible for the plant to complete the vegetative or reproductive stage of its life cycle;
- (ii) such deficiency is specific to the element in question, and can be prevented or corrected only by supplying this element; and.
- (iii) the element is directly involved in the nutrition of the plant quite apart from its possible effects in correcting some unfavorable microbiological or chemical condition of the soil or other culture medium.”

One practical implication of this is that, based on these criteria, a favorable response from adding a given element to the growth medium does not constitute conclusive evidence of its indispensability in plant nutrition (Arnon and Stout 1939). The authors were also aware of some of the theoretical and experimental limitations of their definition, which also led them to state, that, in principle, every element in the periodic table may at some point be shown as being essential to plants (Arnon and Stout 1939). Arnon was also quite aware that different crops, different stages and climatic factors can have different requirement, and that the ‘essentiality’ definition is one of strict physiological function, i.e. it does not necessarily equate with agricultural requirement (Arnon 1952).

In 1952, Arnon proposed that rather than measuring the effect of removal of a nutrient from the medium, an alternative approach to asserting essentiality could be to identify an essential cellular constituent or biochemical reaction in which the element participates (Arnon 1952). A more integrated concept of essentiality would rest on the combined contribution of physiological studies of growth and biochemical studies of functions. Hence, the last criterion was later re-phrased as “...its function or at least its direct effect on the metabolism of the plant must be identified”, and on that basis it was concluded that Na meets the essentiality criteria in the freshwater algae *Anabaena cylindrica* (Allen and Arnon 1955).

Establishing a requirement for minor elements in plant metabolism thus became a fashionable approach. Influenced by this evolution, but also by findings that the 2nd criterion of Arnon and Stout

(1939) may be too rigid, the term *functional nutrient* (or metabolism nutrient) emerged in contrast to essential nutrient, to include any mineral element that functions in plants irrespective of whether its action is specific or indispensable (Nicholas 1961; Bollard and Butler 1966). Interestingly, Nicholas also described five types of experiments needed to establish unequivocal evidence for minor elements to be classed as functional constituents of enzymes. He also predicted, that the agronomic importance of trace metals will increase as less developed areas of the world are brought into crop cultivation. It had become evident that, particularly in the tropics and subtropics, “deficiencies of minor elements in certain areas may account for the disappointing results given by fertilizers and the defective functioning of legumes, thus preventing the establishment of stable systems of farming” (Webb 1959). This is an important point to keep in mind for the debate we are proposing.

Around the same time, Epstein went on to reduce the essentiality criteria to just two: (i) failure to grow normally and to complete the life cycle in a medium purged of the element (as in Arnon and Stout 1939) and (ii) the element is a constituent of a molecule which is known to be an essential metabolite (Epstein 1965). The latter transfers the test of essentiality from the element itself to the metabolite of which it is a part, which of course also has its own difficulties (Epstein 1965). Hence, he also pointed out that any such criteria of essentiality are mental constructs, which are not easy to apply unambiguously in all situations that exist in nature.

Over time, following the ‘functional’ notion, many others have regularly reviewed the evidence for those elements which do not clearly fail or pass the Arnon and Stout criteria of essentiality (Bollard and Butler 1966; Asher 1991; Pilon-Smits et al. 2009; Subbarao et al. 2003). Yet, after Cl was admitted in 1954, only one new element was added to the list of essential elements, Ni in 1987 (Kirkby 2012).

More recently, perhaps around the early 1980 s, the term *beneficial elements* became popular to include elements that stimulate plant growth or health, but have not been shown so far to meet the strict essentiality criteria (Asher 1991; Marschner 1986). Compared to ‘functional’, ‘beneficial’ is perhaps more meaningful in that it implies usefulness or importance of some kind, but not necessarily essentiality, whereas all essential elements are of course also functional.

Arnon had already recognized the many instances where addition of an element might improve agricultural production but not prove essentiality (Arnon 1952).

The definition of ‘essential’ and ‘beneficial’ mineral elements has hardly changed since then. The most recent edition of a leading textbook on plant nutrition, Marschner’s “*Mineral nutrition of higher plants*”, specifies that, for an element to be considered essential, three criteria must be met (Kirkby 2012):

1. A given plant must be unable to complete its life-cycle in the absence of the element.
2. The function of the element must not be replaceable by another element.
3. The element must be directly involved in plant metabolism – for example, as a component of an essential plant constituent such as an enzyme – or it must be required for a distinct metabolic step such as an enzyme reaction.

Only the third criterion differs somewhat from Arnon and Stout (1939), i.e. it represents a necessary evolution in terms of integrating the biochemical role of an element, as discussed above. In contrast, beneficial elements are defined as elements that stimulate growth, but are not essential according to these three criteria, or are essential only for certain plant species, or under specific conditions (Broadley et al. 2012). The latter point, essentiality only in certain species or under certain conditions, leaves much room for interpretation. It may simply not be known yet, and perhaps also causes great confusion among scientists, regulatory bodies, industry and other stakeholders. The distinction between beneficial and essential is especially difficult in the case of some trace elements (Broadley et al. 2012).

### **The consequences of not being a recognized plant nutrient**

Our concern is that the current definition of a plant nutrient constrains the study of plant nutrition as well as the development of fertilization practices needed to optimize the production of foods ideally suited for animal and human diets. Optimization of plant nutrition in the context of a new societal optimum

for nutrients (Scientific Panel on Responsible Plant Nutrition 2020) involves much more than the mere ability to complete a plant's lifecycle.

An important negative consequence of the historically narrow definition of a plant nutrient has been its use as the founding principle underlying the legal definition of fertilizers and plant nutrients, as applied by many regulatory agencies worldwide. The classification of a nutrient as essential, as opposed to beneficial or non-nutrient, profoundly affects all manner of labeling, registration and use guidelines of fertilizers and other nutrient-containing products. Plant nutrients that are agronomically and economically critical for plant development and growth and the production of quality harvested product, but that are not called 'essential', currently fall into a regulatory limbo that constrains scientific inquiry, limits industrial and technological innovations and ultimately reduces plant productivity and quality.

Just to serve as an example, Table 1 illustrates the confusing discrepancy between elements that are termed essential or beneficial nutrients by plant nutritionists (Marschner 2012) and their respective treatment in the current EU fertilizer regulation (EU 2019). In this example, Cl is listed as 'essential' by plant nutrition scientists, whereas it is not classified as a plant nutrient by the EU. In contrast, Co and Na are viewed as 'beneficial' elements in science textbooks, but classified as nutrients by the EU (Table 1).

As another example, the ISO standard on the classification of fertilizers, soil conditioners and beneficial substances (revised version currently under development) strictly refers to the established list of essential elements by defining micronutrient fertilizers as "Fertilizers, which contain one or more of

the elements, such as boron, manganese, iron, zinc, nickel, copper, molybdenum, and/or chlorine, which are essential, in relatively small quantities, for plant growth" (ISO 2021a). Similarly, the new ISO standard on vocabulary defines 'fertilizer' as a "Substance containing one or more recognized plant nutrient(s), which is used for the purpose of providing the plants or mushrooms with nutrients and designed for use or claimed to have value in promoting their growth"; it defines 'plant nutrient' as a "Substance, which is essential for plant growth" (ISO 2021b). While the vocabulary standard includes a definition of 'other nutrient elements' as "Substances that are not required by all plants but can promote plant development and may be essential for particular taxa." (ISO 2021b), they are not included in the classification system for fertilizers, soil conditioners and beneficial substances (ISO 2021a). The ISO standards leave one big question wide open: who 'recognizes' plant nutrients as essential for plant growth?

In the United States, state agencies – not the federal government – determine what is classed as a nutrient, relying on advice from the research community. The Association of American Plant Food Control Officials (AAPFCO) strives to gain at least some uniformity and consensus amongst the various U.S. and Canadian fertilizer regulatory programs. As of today, AAPFCO still primarily adheres to the Arnon and Stout definition for nutrient essentiality.

At times this has bizarre consequences. For example, although numerous reviews and hundreds of scientific articles have been published on silicon's beneficial effects on plant growth, development, abiotic and biotic stress, it is still not recognized as being necessary for plant development by any of these bodies, and thus also not widely used by farmers (Zellener et al. 2021). It appears everyone is waiting for each other to determine what is a plant nutrient and what is not. In contrast, in 2004, the Brazilian Ministry of Agriculture, which regulates commercial production of fertilizers, ruled that Si is an essential micronutrient (Zellener et al. 2021).

More than half of the elements in the periodic table are known to occur in plant tissues and it is likely that with improved analytical techniques many of the remaining ones may be found too (Asher 1991). Who is or can become the trusted global scientific voice that judges if an element is a plant nutrient or not, based on an updated view of the original criteria

**Table 1** Current definition of selected elements as plant nutrients (Marschner 2012) and their respective classification in the current EU Fertilising Products regulation 2019/1009

Elements	Marschner (2012)	EU (FPR 2019/1009)
Al	Beneficial	Not a nutrient
Cl	Essential	Not a nutrient
Co	Beneficial	Nutrient
Na	Beneficial	Nutrient
Ni	Essential	Contaminant
Se	Beneficial	Not a nutrient
Si	Beneficial	Not a nutrient

set by agricultural scientists many decades ago? By what authority can the currently accepted criteria be updated to achieve the optimization of the full scope of food, socioeconomic, environmental and health objectives of a growing global population (Scientific Panel on Responsible Plant Nutrition 2020)?

This discussion matters because an outdated, too strict interpretation of the definition of a plant nutrient impacts the entire human society. At the time of Arnon and Stout (1939), global human population was 2.3 billion and agricultural land was abundantly (made) available. The current world population is 7.9 billion and future food production must primarily rely on sustainable intensification of the existing land (Folberth et al. 2020). Global climatic changes are likely to result in more stressful conditions for crop production, and there are significant needs and opportunities to produce more nutritious food. We believe that a modern definition of what is a ‘plant nutrient’ - grounded in science and relevant in practice - is the foundation for a holistic crop nutrition contribution to food system transformation and sustainable development.

### **Some specific inadequacies of the current definition of a plant nutrient**

Concerns over the interpretation and negative impacts of the strict definition of essentiality were eloquently summarized by Epstein (1999) and others. In his review of silicon, Epstein found the near-universal acceptance of this definition to be puzzling in view of its flaws, suggesting that for criterion (i) many plants may be quite severely deficient in a nutrient element and yet complete their life cycle; (ii) is redundant, and (iii) presumes that designation of an element as essential has to entail knowledge of its direct involvement in the nutrition of the plant (Epstein 1999). As an example, he pointed out that at the time when the essentiality of boron was established (Brenchley and Warington 1927), nothing was known about its direct involvement in plant nutrition. Indeed, it was not until 1996 that the first definitive role of B was defined in plants (reviewed in Brown et al. 2002). Prior to this, the unambiguous evidence of essentiality was simply that the plants failed unless the element was supplied.

The first criterion in the strict definition of an essential nutrient – ‘A given plant must be unable to complete its lifecycle in the absence of the element’ – would suggest that the ability to remove a putative plant nutrient from the experimental environment to such an extent as to disrupt the plant life cycle, is the pre-requisite for the establishment of biological essentiality. It is also worthwhile to mention that such a strict criterion was never applied to defining essential nutrients for animals and humans. This first criterion suggests that essentiality is a matter of technological capabilities and not biological function. By this standard, the most recently identified essential elements (e.g. B, Mo, Cl, Ni), which had been known to be biologically important to plants, were classified as ‘non-essential’ prior to the development of the techniques required to eliminate trace contaminants of these elements from the growth environment. For some elements, e.g. iodine, even air purification would be required to exclude the possible presence of volatile forms of the element, a technique that has not been implemented yet in current plant nutrition research. Both Arnon and Stout (1939) and the authors of Marschner (2012) book recognized that the list of essential elements and the definitions will change over time. They emphasized that the original list of the ‘plant nutrients’ would and should expand, i.e. developments in analytical chemistry and in methods to minimize contamination during growth experiments may lead to a lengthening of the list of essential micronutrient elements and a corresponding shortening in the list of beneficial elements.

Nickel is the most recent example of such development, i.e. an example of the reliance upon new technologies for chemical purification and experimental cleanliness for eliciting deficiency symptoms and functions. Nickel is now considered an essential micronutrient for higher plants although failure to complete the life cycle in the absence of Ni has only been demonstrated in a few plant species (Gerendás et al. 1999). It was initially considered because of its specific function in the enzyme urease, but was added to the list of essential nutrients after report of a reduced germination capacity of Ni-deficient seeds harvested from the third generation of Ni-deprived plants grown in an ultra-clean culture environment with extensive purification of nutrient salts (Brown et al. 1987). Though failure to complete the plant life-cycle has not been demonstrated in the field, Ni

deficiency has been demonstrated to so severely limit the productivity of tree species in several geographies to become economically non-viable (Wood et al. 2004).

A second inadequacy of the strict Arnon and Stout definition is that it ignores the realities of modern agricultural and horticultural production. For some uses, completion of the growth cycle may not be economically meaningful at all (e.g., leafy vegetables, ornamental plants, forest species, landscape plants etc.). Instead, the speed of growth, developmental progression, tolerance to stress conditions, ability to grow under specific environmental conditions, or the production of quality plant products are essential for economic viability. To suggest a nutrient is not a ‘plant nutrient’ from a regulatory and commercial perspective unless the plant lifecycle is completed, even in the presence of clear evidence of biological function and economic importance, artificially constrains productivity and innovation. We do note however, that Arnon and Stout (1939) originally defined their first criterion as “a deficiency of it makes it impossible for the plant to complete the vegetative *or* reproductive stage of its life cycle”, whereas later on this was reduced to just ‘life cycle’ as a whole.

Silicon is a clear example of an element that is essential for the economically viable production of several plant species but that has not been shown to meet criterion 1 of the classic essentiality criteria. Silicon is present in plants in amounts equivalent to those of many macronutrients and evidence suggests that it should be included among the elements having a major bearing on plant life (Epstein 1999). Silicon plays an important role in enhancing plant’s resistance to numerous biotic (e.g. microbial pathogens, herbivores) and abiotic (e.g. salinity, drought, heavy metals, nutrient deficiency, etc.) stresses (Ma and Yamaji 2008; Coskun et al. 2019). The majority of studies demonstrate significant effects of Si on measures such as growth, photosynthesis, enzyme activities, ion and water transport only under stress conditions (Coskun et al. 2019; Zellener et al. 2021). This is further supported by most transcriptomic studies which show large effects of Si on gene expression under stress conditions, but very few effects in the absence of stress (Coskun et al. 2019). It can be argued that non-stress conditions do not really exist for field crops, which inevitably will experience some sorts of stress during their life cycle. For Si accumulator crops such

as rice (*Oryza sativa*), yield benefits from Si fertilizer applications have been well documented (Epstein 1999; Ma and Yamaji 2008). Silicon uptake mutants of rice grow poorly under field conditions (Tamai and Ma 2008). In fact, depletion of plant available Si in paddy soils due to continuous removal of Si by rice crops has been suggested as a cause for declining rice yields in certain situations (Savant et al. 1997).

Based on the current definition, iodine is also not considered an ‘essential element’, but, because of its biological functions may now be considered a plant nutrient too. It is required as an inorganic antioxidant in some algae (Küpper et al. 2008) and at least 30 crops have been described to positively respond in terms of an increase of plant biomass to the addition of iodine at micronutrient levels in nutrient solution (Medrano-Macías et al. 2016). Iodine has been shown to influence N uptake and metabolism, photosynthesis (chlorophyll production, efficiency and CO<sub>2</sub>-fixation as carbohydrates in the leaves and fruits) and anti-oxidant production and oxidative stress-signaling pathways (Kiferle et al. 2021; Gonzali et al. 2017). Phenotypic studies showed the positive effect of iodine in the nutrient solution at micronutrient levels on plant biomass development, timely flowering and fruit formation, and stress resilience, compared to a nutrient solution with iodine concentration below detection level (Kiferle et al. 2021).

Arnon and Stout (1939) also made no claim or specification that an essential element must be essential for all species under all conditions and yet the term ‘essential plant nutrients’ has become accepted as applying to all plant species. This assumption has resulted in some unusual outcomes. For example, while Si meets the Arnon and Stout requirement for essentiality in rice, horsetail (*Equisetum*) and perhaps cucurbits and other Si rich species, and has very clear biological benefit to a broad array of species, it is not included in the list of essential elements in most modern textbooks. A wider point to make here is that different evolutionary clades of plants can display quite distinct mineral compositions (Neugebauer et al. 2018; Jansen et al. 2002). Composition does not, of course, equate to essentiality, but there is surely still a lot to be learned beyond the small number of species that are typically studied.

The third criterion is also problematic as it fails to recognize that the growing conditions for the species in their native environment might impose

a unique constraint that is uniquely overcome by the uptake of a particular nutrient. In the absence of the constraints present in the natural environment, that same element may show no benefit and hence, by this definition, could not be considered essential. The particular inadequacy of this has recently been illustrated for tea (*Camellia sinensis*), a species that is adapted to acid soils, and for which  $\text{Al}^{3+}$  is essential for root growth and development in all the tested varieties. In the absence of  $\text{Al}^{3+}$ , tea plants failed to generate new roots which is clearly a requirement for normal growth, development and ultimately plant survival (Sun et al. 2020). To suggest that the essentiality of an element can only be established in the artificial circumstance of a highly purified culture media, but not in the natural growing conditions is problematic as it is well known that the prevalent growing condition can dramatically affect the sensitivity of a species to a nutrient deficiency. Thus, Co, Ni and Mo are required in greater amounts in N fixing species; Ni is required in greater amounts when urea or ammonia are the dominant N source; Si is highly beneficial when Mn is present at toxic levels, and so on.

Epstein (1999) also argued that the three requirements for essentiality were redundant and not reflective of the biological importance of several elements. Selenium, for example, fulfills criterion 3 as it is present at the catalytic center of several antioxidant enzymes, such as glutathione peroxidase (Martins Alves et al. 2020; Fajardo et al. 2014) and may play a wide variety of other biological roles, particularly in stress tolerance (Fichman et al. 2018). Iodine also appears to satisfy criterion 2 and 3. It was recently demonstrated that I uniquely up- or down-regulated 579 genes and that *Arabidopsis* (*Arabidopsis thaliana*) contains 82 iodinated proteins in root and shoot, many of which are involved in several fundamental biochemical processes, and that is not observed when the closely related halogen bromine is included in the nutrient solution (Kiferle et al. 2021). While Si may not meet criterion 3 strictly, the deposition of Si in the apoplast forming an obstruction barrier for biotic and abiotic stressors underpins many of the reported functions of Si in plants (Coskun et al. 2019), and this role is biologically important.

## Expanding the scope

A question may be raised as to whether we should think even more broadly beyond the direct beneficial or essential roles of mineral elements in plants as discussed above. This could include a consideration of the role that nutrients in the environment can play in enhancing plant productivity even when that element is not-essential and has no specific role in a plant metabolic process. The comments made below are meant to be provocative, indicating potential additional considerations for a new definition over the longer term.

The establishment of the current essential plant nutrients has largely been achieved by growing plants in highly refined culture media under controlled experimental conditions. This approach is fundamentally divorced from the reality of agricultural production or natural environments in which environmental stress, nutrient interactions and the microbiome all affect plant performance. At the time of Arnon and Stout, little was known about the fundamental role that the plant microbiome plays in plant productivity and adaptation to stress. We now know that plant-associated microbiomes confer fitness advantages to the plant host, including growth promotion, nutrient uptake, stress tolerance and resistance to pathogens (Trivedi et al. 2020). Given the critical role the plant microbiome plays in all that, one might hypothesize that a nutrient ‘essential for the microbiome’ would in turn also be critical for optimal plant productivity, particularly under stress. Nutrient elements that are essential for microbiome function, for which the role of Co for rhizobium is an example, may in turn influence plant microbiome activity and hence crop productivity (Okamoto and Eltis 2011). Such effects would also not readily be observed in the artificial culture conditions usually employed in studies of the essential elements.

Elements of interest that are known to have biological function in a range of organisms include: Br, which naturally occurs in 3200+ organohalogen (Gribble 1999) from a variety of species and is known to be essential for tissue development and membrane architecture in animals (McCall et al. 2014); Co which is known to have a broad array of functions in microbial and animal systems (Kobayashi and Shimizu 1999); Se which is essential for bacteria, animals and at least in some plants is beneficial for plant growth (Gupta and Gupta 2017); I



and Si as described above; V (vanadium) which has function in several nitrogen fixing bacteria and peroxidases from many taxonomic groups (Tanabe and Nishibayashi 2019).

Another consideration in the discussion of what is a plant nutrient could relate to the question of whether we define a plant nutrient as solely an inorganic element, or as a simple molecule? In animal and human biology the definition of a ‘nutrient’ is far more inclusive than it is in plant nutrition. The Merriam Webster definition of a nutrient is “a substance that is needed for healthy growth, development, and functioning”. This definition uses the terminology ‘substance’ since it includes organic nutrient substances required by heterotrophic organisms that the organism itself cannot synthesize (proteins, amino acids, fats, vitamins, minerals, carbohydrates etc.).

In classical plant nutrition the term ‘plant nutrients’ generally refers to the known essential mineral elements, either in their elemental state or as the molecular form as acquired by the plant (e.g. nitrate, ammonium, phosphate, borate/boric acid, molybdate, sulfate etc.). In common usage, though not legal usage, the term ‘beneficial plant nutrient’ could also be used to describe elements that have a positive effect on the healthy growth, development, and functioning of the plant (e.g. I, Si, Co, Na). Central to the definition of what is a ‘plant’ nutrient is the specification that an element be required for life cycle completion. This differs fundamentally from the definition of nutrient as used in animal or human nutrition, which does not specify that the organism cannot survive in the absence of the nutrient, only that it will not be ‘healthy’.

There is also no current consideration that organic molecules synthesized outside the plant may function as ‘plant nutrients’ in the fashion that vitamins and other organic molecules are considered as nutrients to heterotrophs. Evidence of the clear stimulatory effects of plant growth promoting rhizobacteria and growing evidence that some biostimulants can stimulate plant growth by means other than their essential nutrient content (Du Jardin 2015; Yakhin et al. 2017) may suggest that molecules synthesized ex-planta might also function as plant ‘nutrients’. The possibility that discrete organic molecules, or complex inorganic molecules may be critical for plant growth and development has not been rigorously explored, but should

at least be considered in the future, in the broad redefining of what is a plant nutrient.

Although these are all worthy topics for further debate, we propose to first focus attention on elements of the periodic table and their direct role as plant nutrients. Future definitions could also consider other (mineral or organic) substances that have clear beneficial effects on plants and their uses, or microbial functions affecting plants.

### Moving forward

The purpose of the proposed debate is not to re-define the term ‘essential element’ (or essential plant nutrient). Instead, we propose, perhaps for the first time, to properly define the term ‘plant nutrient’, through a single definition that encapsulates both elements that are essential and beneficial for plants, as well as those that are important for other uses, such as animal and human nutrition. A proposed new definition might therefore read:

A mineral plant nutrient is an element which is essential or beneficial for plant growth and development or for the quality attributes of the harvested product of a given plant species grown in its natural or cultivated environment. A plant nutrient may be considered essential if the life cycle of a diversity of plant species cannot be completed in the absence of the element. A plant nutrient may be considered beneficial if it does not meet the criteria of essentiality, but can be shown to benefit plant growth and development or the quality attributes of a plant or its harvested product.

This definition should be viewed as a starting point for further debate, but it has some interesting features. It includes (i) elements currently identified as essential, (ii) elements for which a clear plant metabolic function has been identified (even if the first criteria of failure to complete the lifecycle has not been demonstrated), as well as (iii) elements that have demonstrated clear benefits to plant productivity, crop quality, resource use efficiency, or plant stress tolerance. Besides emphasis on plant biomass (yield), it also covers benefits in terms of plant health (e.g. tolerance to abiotic stresses or resistance to pests and diseases) and the quality of the harvested commercial products for their different

end uses. This also provides a much needed opportunity to link plant nutrition more directly to animal and human nutrition, a requirement that was stated a long time ago (Hoagland and Arnon 1948).

Reframing the definition around the term ‘plant nutrient’ and emphasizing that this explicitly includes both the essential and the demonstrated beneficial mineral elements provides greater clarity. It will enable regulators to consider the beneficial elements as legitimate fertilizer components, while encouraging more scientific inquiry for optimizing yield and quality oriented plant production strategies in different species and environments. It would likely also increase commercial activity. None of this would diminish the Arnon and Stout principles, but rigor must be applied to avoid a flurry of unproven claims, or ‘snake oils’ being sold. Hence, it is important that the beneficial nutrients would need to satisfy clear criteria and demonstration (likely for a specific species, environment or function).

The definition allows for future discoveries of elements and it includes the possibility that a plant nutrient may have environmental and/or plant specificity, such as  $Al^{3+}$  for tea in acid soils, Co or V for associative N fixation, or Si or Se under stress conditions.

We propose an open scientific debate on the refinement and implementation of this updated definition of plant nutrients. Another key outcome of this debate could be a more precise definition of the modern experimental evidence required to classify an element as a plant nutrient. Particular emphasis must be placed on the concrete tests to perform for beneficial elements, but there is also need to refine those for essential elements. It has long been considered, for example, that Na and Si should also be classed as essential plant nutrients as essentiality has already been established in some plant species (Kirkby 2012; Bollard and Butler 1966; Epstein 1999; Subbarao et al. 2003).

While such tests should continue to place the major emphasis on the functions of nutrients in the plant, they must also recognize that we may not know the precise functions yet, even if we observe clear benefits to the plant. The scientific community should draw up a robust protocol for the necessary tests to perform in the laboratory, the field and natural environments, based on the most advanced scientific methodologies and techniques. The tests could include – besides the phenotypical response of the plant to the addition or removal of the candidate

nutrient from its environment - also regulation of gene-expression and post-translational responses in the proteome, or changes in enzyme activity to explain the observed phenotypical response.

An independent global body of scientists – for example through the International Plant Nutrition Council – could be given the mandate to periodically review such new evidence, update the list of essential and beneficial plant nutrients, and thus also guide policy makers and industry more directly in making the right decisions for improving nutrition. As the leading global association with more than 400 members encompassing all actors in the fertilizer value chain, the International Fertilizer Association (IFA) could act as an important stakeholder and facilitator of a platform to implement the outcomes of these discussions.

We believe that a rethinking of the definition of plant nutrients would lead to several positive outcomes:

- Scientists will be incentivized to further look for new plant nutrients and study their functions and interactions with plant productivity and efficiency.
- The fertilizer industry will have greater opportunities for differentiation of products, collaborative research and business innovation.
- Farmers will be freed to more fully explore the holistic vision of ‘plant nutrition’ that includes integrated roles of plant nutrients on stress tolerance, efficiency of resource use, crop quality and whole system sustainability.
- Consumers will benefit from enhanced productivity and food that could be a lot more nutritious.
- Regulators and government agencies will achieve a more nuanced, integrative, adaptable and modern interpretation of what is a plant nutrient.

We wish to invite everyone to participate in an open discussion and share their general views and specific suggestions at <https://www.sprpn.org/debate>, through e-mails to the corresponding author, or through commentaries in the journal. A wonderful example for such a debate can be found in recent issues of the *New Phytologist*. Lewis argued that an alternative interpretation of published evidence suggests that B – listed as an essential plant nutrient for nearly 100 years – would not be in compliance with one of the criteria for essentiality, but should instead be viewed as potentially toxic (Lewis 2020b). Spirited, thoughtful responses

(González-Fontes 2020; Wimmer et al. 2020; Lewis 2020a; McGrath 2020) made it clear that there is still a lot to be learned about this particular nutrient. However, despite the excellent scientific discourse, the discussion on B did not resolve the fundamental definition problem we are hoping to tackle here.

## Dedication

This paper is dedicated to Professor Emanuel Epstein, a close colleague and mentor to one of the authors (PHB) and a leading light in plant nutrition for more than 80 years. Emanuel Epstein commenced his study of plant nutrition in the illustrious laboratory of Dennis Hoagland at University of California, Berkeley in 1942 under the direction of Perry Stout, who with Daniel Arnon had developed the 1939 definition of nutrient essentiality that is the focus of this paper. Professor Epstein joined the Department of Soils and Plant Nutrition at the University of California at Davis in 1958 where he continues to be actively engaged, including reviewing and commenting on this manuscript. Professor Epstein is nearing his 105th birthday. He has made many seminal contributions to plant nutrition, e.g., being the first to demonstrate that nutrient ions are absorbed by plant roots in a fashion akin to enzymatic catalysis, thereby initiating the study of ion transporters in plants. Prof. Epstein has also made many seminal contributions in the field of salinity and was a leading force in the recognition of the critical role of silicon as a plant nutrient. The lead author (PHB) has had the pleasure of many spirited discussions with Emanuel on how an adherence to the Arnon and Stout principle of essentiality constrains the field of plant nutrition.



It is an honor to offer this opinion paper as a tribute to Professors Epstein's many contributions the field of plant nutrition.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Allen MB, Arnon DI (1955) Studies on nitrogen-fixing blue-green algae. II. The sodium requirement of *Anabaena cylindrica*. *Physiol Plant* 8:653–660. <https://doi.org/10.1111/j.1399-3054.1955.tb07758.x>
- Arnon DI (1952) Growth and function as criteria in determining the essential nature of inorganic nutrients. In: Truog E (ed) *Mineral nutrition of plants*. University of Wisconsin Press, Madison, pp 313–341
- Arnon DI, Stout PR (1939) The essentiality of certain elements in minute quantity for plants with special reference to copper. *Plant Physiol* 14:371–375. <https://doi.org/10.1104/pp.14.2.371>
- Asher CJ (1991) *Beneficial elements, functional nutrients, and possible new essential elements, Micronutrients in agriculture*. Soil Science Society of America, Madison, pp 703–730
- Bollard EG, Butler GW (1966) Mineral nutrition of plants. *Annu Rev Plant Physiol* 17:77–112. <https://doi.org/10.1146/annurev.pp.17.060166.000453>
- Brenchley WE, Warington K (1927) The role of boron in the growth of plants. *Ann Bot* 41:167–187
- Broadley MR, Brown PH, Cakmak I, Ma JF, Rengel Z, Zhao FJ (2012) Chapter 8 - Beneficial elements. In: Marschner P (ed) *Marschner's mineral nutrition of higher plants*, 3rd edn. Academic, Amsterdam, pp 249–269
- Brown PH, Bellaloui N, Wimmer MA, Bassil ES, Ruiz J, Hu H, Pfeffer H, Dannel F, Römheld V (2002) *Plant Biol* 4(2):205–223
- Brown PH, Welch RM, Cary EE (1987) Nickel: a micronutrient essential for higher plants. *Plant Physiol* 85:801–803. <https://doi.org/10.1104/pp.85.3.801>
- Byerlee D (2021) The super state: the political economy of phosphate fertilizer use in South Australia, 1880–1940. *Jahrb Wirtsch / Economic History Yearbook* 62:99–128. <https://doi.org/10.1515/jbwg-2021-0005>
- Coskun D, Deshmukh R, Sonah H, Menzies JG, Reynolds O, Ma JF, Kronzucker HJ, Bélanger RR (2019) The

- controversies of silicon's role in plant biology. *New Phytol* 221:67–85. <https://doi.org/10.1111/nph.15343>
- de Saussure T (1804) *Recherches chimiques sur la végétation*. Nyon, Paris
- Du Jardin P (2015) Plant biostimulants: definition, concept, main categories and regulation. *Sci Hortic* 196:3–14. <https://doi.org/10.1016/j.scienta.2015.09.021>
- Epstein E (1965) Mineral metabolism. *Plant Biochemistry*. Elsevier, Amsterdam, pp 438–466
- Epstein E (1999) Annual review of plant physiology and plant molecular biology. *Silicon* 50:641–664. <https://doi.org/10.1146/annurev.arplant.50.1.641>
- EU (2019) Regulation (EU) 2019/1009 of the European Parliament and of the Council of 5 June 2019 laying down rules on the making available on the market of EU fertilising products. <https://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX%3A32019R1009>. Accessed 14 Oct 2021
- Fajardo D, Schlautman B, Steffan S, Polashock J, Vorsa N, Zalapa J (2014) The American cranberry mitochondrial genome reveals the presence of selenocysteine (tRNA-Sec and SECIS) insertion machinery in land plants. *Gene* 536:336–343. <https://doi.org/10.1016/j.gene.2013.11.104>
- Fichman Y, Koncz Z, Reznik N, Miller G, Szabados L, Kramer K, Nakagami H, Fromm H, Koncz C, Zilberstein A (2018) SELENOPROTEIN O is a chloroplast protein involved in ROS scavenging and its absence increases dehydration tolerance in *Arabidopsis thaliana*. *Plant Sci* 270:278–291. <https://doi.org/10.1016/j.plantsci.2018.02.023>
- Folberth C, Khabarov N, Balkovič J, Skalský R, Visconti P, Ciais P, Janssens IA, Peñuelas J, Obersteiner M (2020) The global cropland-sparing potential of high-yield farming. *Nat Sustain* 3:281–289. <https://doi.org/10.1038/s41893-020-0505-x>
- Gerendás J, Polacco JC, Freyermuth SK, Sattelmacher B (1999) Significance of nickel for plant growth and metabolism. *J Plant Nutr Soil Sci* 162:241–256. [https://doi.org/10.1002/\(SICI\)1522-2624\(199906\)162:3<241::AID-JPLN241>3.0.CO;2-Q](https://doi.org/10.1002/(SICI)1522-2624(199906)162:3<241::AID-JPLN241>3.0.CO;2-Q)
- González-Fontes A (2020) Why boron is an essential element for vascular plants: A comment on Lewis (2019) 'Boron: the essential element for vascular plants that never was'. *New Phytol* 226:1228–1230. <https://doi.org/10.1111/nph.16033>
- Gonzali S, Kiferle C, Perata P (2017) Iodine biofortification of crops: agronomic biofortification, metabolic engineering and iodine bioavailability. *Curr Opin Biotechnol* 44:16–26. <https://doi.org/10.1016/j.copbio.2016.10.004>
- Gribble GW (1999) The diversity of naturally occurring organobromine compounds. *Chem Soc Rev* 28:335–346. <https://doi.org/10.1039/A900201D>
- Gupta M, Gupta S (2017) An overview of selenium uptake, metabolism, and toxicity in plants. *Front Plant Sci* 7:2074. <https://doi.org/10.3389/fpls.2016.02074>
- Hoagland DR, Arnon DI (1948) Some problems of plant nutrition. *Sci Monthly* 67:201–209
- ISO (2021a) International Standard ISO/DIS 7851 Fertilizers, soil conditioners and beneficial substances —Classification. ISO. <https://www.iso.org/standard/77570.html>. Accessed 14 Oct 2021
- ISO (2021b) International Standard ISO/DIS 8157 Fertilizers, soil conditioners and beneficial substances - Vocabulary. ISO. <https://www.iso.org/standard/80949.html>. Accessed 14 Oct 2021
- Jansen S, Broadley MR, Robbrecht E, Smets E (2002) Aluminum hyperaccumulation in angiosperms: a review of its phylogenetic significance. *Bot Rev* 68:235–269. [https://doi.org/10.1663/0006-8101\(2002\)068\[0235:AHIAAR\]2.0.CO;2](https://doi.org/10.1663/0006-8101(2002)068[0235:AHIAAR]2.0.CO;2)
- Küpper FC, Carpenter LJ, McFiggans GB, Palmer CJ, Waite TJ, Boneberg E-M, Woitsch S, Weiller M, Abela R, Grolimund D, Potin P, Butler A, Luther GW, Kroneck PMH, Meyer-Klaucke W, Feiters MC (2008) Iodide accumulation provides help with an inorganic antioxidant impacting atmospheric chemistry. *Proc Natl Acad Sci* 105:6954–6958. <https://doi.org/10.1073/pnas.0709959105>
- Kiferle C, Martinelli M, Salzano AM, Gonzali S, Beltrami S, Salvadori PA, Hora K, Holwerda HT, Scaloni A, Perata P (2021) Evidences for a nutritional role of iodine in plants. *Front Plant Sci* 12:616868. <https://doi.org/10.3389/fpls.2021.616868>
- Kirkby EA (2012) Chapter 1: Introduction, definition and classification of nutrients. In: Marschner P (ed) *Marschner's mineral nutrition of higher plants*, 3rd edn. Academic, Amsterdam, pp 3–5
- Knop W (1860) Über die Ernährung der Pflanzen durch wässrige Lösungen bei Ausschluss des Bodens. *Landw Versuchsst* 2:65–99
- Kobayashi M, Shimizu S (1999) Cobalt proteins. *Eur J Biochem* 261:1–9. <https://doi.org/10.1046/j.1432-1327.1999.00186.x>
- Lawes JB, Gilbert JH (1851) On agricultural chemistry, especially in relation to the mineral theory of Baron Liebig. *J R Agric Soc* 12:1–40
- Lewis DH (2020) The status of boron as an essential element for vascular plants: I. A response to González-Fontes (2020) 'Why boron is an essential element for vascular plants'. *New Phytol* 226:1231. <https://doi.org/10.1111/nph.16030>
- Lewis DH (2020) The status of boron in relation to vascular plants. *New Phytol* 226:1238–1239. <https://doi.org/10.1111/nph.16128>
- Ma JF, Yamaji N (2008) Functions and transport of silicon in plants. *Cell Mol Life Sci* 65:3049–3057. <https://doi.org/10.1007/s00018-008-7580-x>
- Macy P (1936) The quantitative mineral nutrient requirements of plants. *Plant Physiol* 11:749–764. <https://doi.org/10.1104/pp.11.4.749>
- Marschner H (1986) *Mineral nutrition of higher plants*. Academic, London
- Marschner P (ed) (2012) *Marschner's mineral nutrition of higher plants*, 3rd edn. Academic, Amsterdam
- Martins Alves AM, Pereira Menezes Reis S, Peres Gramacho K, Micheli F (2020) The glutathione peroxidase family of *Theobroma cacao*: Involvement in the oxidative stress during witches' broom disease. *Int J Biol Macromol* 164:3698–3708. <https://doi.org/10.1016/j.ijbiomac.2020.08.222>
- McCall AS, Cummings CF, Bhave G, Vanacore R, Page-McCaw A, Hudson BG (2014) Bromine is an essential

- trace element for assembly of collagen IV scaffolds in tissue development and architecture. *Cell* 157:1380–1392. <https://doi.org/10.1016/j.cell.2014.05.009>
- McGrath SP (2020) Arguments surrounding the essentiality of boron to vascular plants. *New Phytol* 226:1225–1227. <https://doi.org/10.1111/nph.16575>
- Medrano-Macías J, Leija-Martínez P, González-Morales S, Juárez-Maldonado A, Benavides-Mendoza A (2016) Use of iodine to biofortify and promote growth and stress tolerance in crops. *Front Plant Sci* 7:1146. <https://doi.org/10.3389/fpls.2016.01146>
- Neugebauer K, Broadley MR, El-Serehy HA, George TS, McNicol JW, Moraes MF, White PJ (2018) Variation in the angiosperm ionome. *Physiol Plant* 163:306–322. <https://doi.org/10.1111/pp1.12700>
- Nicholas DJD (1961) Minor mineral nutrients. *Annu Rev Plant Physiol* 12:63–90. <https://doi.org/10.1146/annurev.pp.12.060161.000431>
- Nortcliff S, Gregory PJ (2013) The historical development of studies on soil-plant interactions. In: Gregory PJ, Nortcliff S (eds) *Soil conditions and plant growth*. Wiley-Blackwell, Chichester, pp 1–21
- Okamoto S, Eltis LD (2011) The biological occurrence and trafficking of cobalt. *Metallomics* 3:963–970. <https://doi.org/10.1039/c1mt00056j>
- Pilon-Smits EAH, Quinn CF, Tapken W, Malagoli M, Schiavon M (2009) Physiological functions of beneficial elements. *Curr Opin Plant Biol* 12:267–274. <https://doi.org/10.1016/j.pbi.2009.04.009>
- Sachs J (1865) *Handbuch der Experimental-Physiologie der Pflanzen: Untersuchungen über die allgemeinen Lebensbedingungen der Pflanzen und die Functionen ihrer Organe*. W. Engelmann, Leipzig
- Savant NK, Datnoff LE, Snyder GH (1997) Depletion of plant-available silicon in soils: a possible cause of declining yields. *Commun Soil Sci Plant Anal* 28:1245–1252
- Scientific Panel on Responsible Plant Nutrition (2020) A new paradigm for plant nutrition. Issue Brief 01. <https://www.sprpn.org/issue-briefs>. Accessed 14 Oct 2021
- Subbarao GV, Ito O, Berry WL, Wheeler RM (2003) Sodium—a functional plant nutrient. *Crit Rev Plant Sci* 22:391–416. <https://doi.org/10.1080/07352680390243495>
- Sun L, Zhang M, Liu X, Mao Q, Shi C, Kochian LV, Liao H (2020) Aluminium is essential for root growth and development of tea plants (*Camellia sinensis*). *J Integr Plant Biol* 62:984–997. <https://doi.org/10.1111/jipb.12942>
- Suttle NF (2010) *Mineral nutrition of livestock*, 4th edn. CABI, Wallingford
- Tamai K, Ma JF (2008) Reexamination of silicon effects on rice growth and production under field conditions using a low silicon mutant. *Plant Soil* 307:21–27. <https://doi.org/10.1007/s11104-008-9571-y>
- Tanabe Y, Nishibayashi Y (2019) Recent advances in nitrogen fixation upon vanadium complexes. *Coord Chem Rev* 381:135–150. <https://doi.org/10.1016/j.ccr.2018.11.005>
- Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK (2020) Plant-microbiome interactions: from community assembly to plant health. *Nat Rev Microbiol* 18:607–621. <https://doi.org/10.1038/s41579-020-0412-1>
- Van der Ploeg RR, Böhm W, Kirkham MB (1999) On the origin of the theory of mineral nutrition of plants and the law of the minimum. *Soil Sci Soc Am J* 63:1055–1062
- von Liebig J (1840) *Die Chemie in ihrer Anwendung auf Agricultur und Physiologie*. Verlag Vieweg, Braunschweig
- Webb RA (1959) Problems of fertilizer use in tropical agriculture. *Outlook Agric* 2:103–113. <https://doi.org/10.1177/003072705900200302>
- Wimmer MA, Abreu I, Bell RW, Bienert MD, Brown PH, Dell B, Fujiwara T, Goldbach HE, Lehto T, Mock H-P, von Wirén N, Bassil E, Bienert GP (2020) Boron: an essential element for vascular plants: A comment on Lewis (2019) ‘Boron: the essential element for vascular plants that never was’. *New Phytol* 226:1232–1237. <https://doi.org/10.1111/nph.16127>
- Wood BW, Reilly CC, Nyczepir AP (2004) Mouse-ear of pecan: a nickel deficiency. *HortSci* 39:1238–1242. <https://doi.org/10.21273/HORTSCI.39.6.1238>
- Yakhin OI, Lubyantov AA, Yakhin IA, Brown PH (2017) Biostimulants in plant science: a global perspective. *Front Plant Sci* 7:2049. <https://doi.org/10.3389/fpls.2016.02049>
- Zellener W, Tubana B, Rodrigues FA, Datnoff LE (2021) Silicon’s role in plant stress reduction and why this element is not used routinely for managing plant health. *Plant Dis*. <https://doi.org/10.1094/PDIS-08-20-1797-FE>

**Publisher’s Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.