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BOOK REVIEW

A NEW ENCYCLOPEDIC ACCOUNT OF PLANT NUTRITION: BROAD, BRILLIANT, BUT ALSO FLAWED[1]

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In the age of Atkins and the South Beach diet, supermarket shelves overflowing with vitamin and mineral supplements, and an ever-increasing understanding of the link between diet and well-being, development of disease, and lifespan, few would doubt the fundamental importance of nutritional science. Yet, among plant biologists, the study of plant nutrition is considered esoteric and incidental by far too many. It should, of course, be evident that no measurement of biochemical activity, transcript abundance, or physiological response in plants is meaningful without a precise definition of how the organisms or tissue preparations under study were reared and treated nutritionally. For this reason, any modern treatise of the subject area of plant nutrition is a welcome, and necessary, addition to the bookshelves.

Two leading authorities, professors E. Epstein and A. J. Bloom, have now added to this limited arsenal with the long-awaited second edition of *Mineral Nutrition of Plants: Principles and Perspectives.* The book is a valuable and thorough, albeit not perfect, account of the field and deserves adoption by libraries, ion transport researchers, and teachers of upper-level university courses of plant nutrition.

The authors are highly acclaimed in the field, and readers benefit in particular from Epsteins's expertise in basic ion flux analysis and potassium and silicon relations, and Bloom's strong ecophysiological interests.

The book is well written and makes an erudite and ultimately successful case for the fundamental importance of mineral nutrition. A particular strength of the book lies in the thorough historical accounts that accompany each chapter. A clear philosophy penetrates that much is to be learned from experiments conducted by early workers. This approach is refreshing against the matrix of increasingly ahistorical approaches in much of modern science, and the approach is especially appreciated by this referee. Fascinating statistics, examples and analogies abound, and they make for an interesting read in an area that is not considered naturally captivating by many. The book is also attractively illustrated: the blend of representative tables and graphs, micrographs, and technical drawings of plant morphology, postulated ion transport mechanisms, and plant culture systems is above the norm. The breakdown of topics is logical, although the discussion of the roles of individual nutrients and their deficiency symptoms is somewhat disjointed, and details have to be assembled from various chapters.

Epstein and Bloom cover basic mineral nutrition, physiology of ion transport, molecular biology of transport, and, in addition, examine tie-ins with environmental stress, population biology, and climate change. As such, coverage is broad and in many ways both traditional and up-to-date, but not consistently so. In several areas, recent key developments are missed, and often excessive emphasis is placed on the authors' own contributions. The authors are somewhat less prepared to critically appraise the limitations of their own contributions than they are those of others. In this way, the book is radically more personal, and opinionated, than other major treatises of the field, such as Mengel and Kirkby's (2001) *Principles of Plant Nutrition* or the late Horst Marschner's classic *Mineral Nutrition of Higher Plants* (1995), and is best used alongside these resources rather than as a complete replacement.

In the following, I will discuss the merits of individual chapters, guided, naturally, by my own biases—the biases of an ion transport researcher with particular interest in nitrogen and the fundamental workings of ion fluxes.

Chapter 1: Introduction & history—The historical overview here is exceptional, beautifully referenced, and well worth a read even for those who do not wish to venture further into the book or the discipline. The authors discuss the development of the discipline, taking us back as far as Aristotle and Democrit, da Vinci, and phlogiston. This treatment could hardly be done better. Fitting space is given to Stephen Hales' brilliant and arrestingly illustrated *Vegetable Staticks* (Hales, 1727), Boussingault's discovery of nitrogen fixation, and the section culminates in an amusing contrasting of von Liebig's and Hoagland's relative contributions. This contrast is a fine example of the authors' personal, and at times proudly opinionated, approach to the discussion of the discipline and its history: Liebig here receives staunch criticism, while Hoagland gets off easy.

Chapter 2: The media of plan nutrition—Broad evolutionary thoughts precede the discussion of the major nutrient mixes used today. There are excellent diagrams here, and plant culture techniques, from solid media to nutrient-film techniques, hydroponics, and aeroponics, are discussed in better detail than in any of the competitor books. Many good statistics (especially good for those teaching ion transport courses) are included, such as Jackson's global estimate of fine root length (Jackson et al., 1997). The reproduction of Reisenauer's famous survey of soil solution compositions (Reisenauer, 1966) is eminently useful. Most welcome (to me), and amusing, is the warning against the now far too, and non-critical, widespread use of Murashige-Skoog medium in plant research! A small caveat nevertheless must be added here: The authors tend to overstate their case in this section, as evidenced

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by the statement that the rhizosphere of plants is the least explored of all ecosystems, less even than those of deep-ocean trenches (p. 18). With estimates of deep-ocean species yet to be discovered numbering in the millions (possibly in excess of ten million; Grassle and Maciolek, 1992), saying little about their interactions or individual physiologies, this example is not too aptly chosen, however enamored one is (such as this referee) with plant nutrition.

Chapter 3: Inorganic components of plants—The authors briefly (very briefly) describe each essential plant nutrient and engage in an excellent discussion of the difficulty of defining the essentiality of a nutrient. In the process, they abandon the traditional definition by Arnon and Stout (1939). Instead, a new definition of essentiality is given, and its superiority to the old definition is clear. The authors correctly caution against the utility of visual diagnosis of deficiency symptoms (nevertheless shown in color plates for tomato), driving home, in this highly appropriate context, the important distinction between phloem-mobile and -immobile elements. The graded-additions approach for nutrients is discussed, and a good case is made for nutrient-ratio diagnosis systems, such as ''DRIS,'' rather than a focus on any one nutrient in deficiency analyses. Clearly, this chapter opens some discussions that are absent from other leading books in the field, and there is more detail on individual nutrients later in the book (such as in chapter 8), augmenting the utility of the book on this front.

Chapter 4: Nutrient absorption by plants—A pleasant, if basic, description of membranes and cell wall structure is given, the historical development of the distinction between passive and active transport is traced well, and fundamental principles such as the lyotropic series of ions and the enzyme concept of transport are introduced competently. Epstein essentially pioneered the use of the Langmuir isotherm formalism (better known as Michaelis-Menten kinetics) in plant nutrient absorption, and it is good to see the context of these profound contributions given by the originator himself. It is not inappropriate here to focus largely on this early work, but, in the process, a critical discussion of the potential pitfalls of ion flux measurements is sadly omitted. Recent discussions by Britto and Kronzucker (2001, 2003a, b) provide some details of these pitfalls, and this is important here; the face value of ion transport isotherms can often be misleading, and it is certainly dangerous to make direct mechanistic inferences from rubidium transport isotherms obtained with excised barley roots to the crystallography data of Doyle's potassium channels from animal systems (Doyle et al., 1998). It would have been useful here to discuss recent claims of dual-affinity transporters (Fu and Luan, 1998; Kim et al., 1998), the importance, and variability, of ion efflux, issues regarding simplified ion mixtures used during uptake protocols, excised vs. intact roots, and tissue heterogeneity. The presented, and apparently recommended, flux measurement protocols are outdated, and, in practice, they are afflicted at times by substantial error. On p. 92, a major thermodynamic blunder occurs: the Nernst equation is used to demonstrate that only one extra (non-charge-balanced) ion against a background of 100 000 taken up by a cell can change the plasma membrane potential by as much as 100 mV; however, such conclusions cannot be drawn using such an analysis, and this section will therefore compromise the understanding of readers who may attempt to deconstruct the statement: In reality, the Faraday equation, which considers plasma membrane capacitance, is needed for the argument attempted here (see Nobel, 1999, or Gerendás and Schurr, 1999, for a proper discussion of this argument).

Chapter 5: Upward movement of water and nutrients—This chapter begins beautifully with a morphological discussion of cell-to-cell connections (especially plasmodesmata) and the tracheids and vessels in the service of long-distance transport. A good evolutionary context is provided. It is only a minor detractor that the per-gram transpiration figure here is different from one elsewhere in the book. The cohesion theory is thankfully not taken as firmly established, and several key points of criticism are mentioned. The Crafts-Broyer hypothesis forms the center of the discussion of what is known about radial transfer of nutrients to the xylem, and this section is done very well. The Hylmö test-tube model is featured, as are Collander's classic experiments on differential exclusion of ions in long-distance transfer between species. Issues of the relationship between transpiration and ion uptake, periodicity of translocation, and the role of growth hormones also receive coverage. The authors convincingly convey, in a well-referenced way, a picture that much more work is needed in this area before any book on the subject may be closed with confidence.

Chapter 6: Downward movement of food and nutrients—Here, again, the authors take a fitting historical approach, beginning with the girdling experiments of Dixon and Ball (1922) and Mason and Maskell (1928), later isotope-labeling techniques, and the aphid stylet technique developed by Kennedy and Mittler (1953). A good morphological discussion accompanies the physiology of phloem transport. Münch's pressure flow hypothesis is explained well, and recent literature on phloem loading and unloading is summarized successfully (even though Poiseuille's name experiences a spelling mishap), focusing on details of elegant key experiments, and recommending excellent reviews on the subject for further reading. A good chapter.

Chapter 7: Nitrogen and sulfur: a tale of two nutrients—Here, things get more metabolic and biochemical than elsewhere in the book, and, while the metabolic diagrams are attractive, some reservations are in order. The strongest part of the chapter is the discussion of nitrogen fixation, leaning as it does on the outstanding review on the topic by IRRI's N fixation specialists, Ladha and Reddy (2003). The ecophysiology and genetics of N fixation come across exceptionally well, and diagrams here are particularly arresting. Far shorter is the discussion of mycorrhizal associations—this is delayed until later in the book, with emphasis on phosphorus, not inappropriately so. The discussion of NO_3^- and NH_4^+ acquisition is plagued by a lack of careful research: for instance, the claim is made (p. 178) that cytoplasmic pH is lowered by NH_4^+ uptake, an observation that is not borne out in the literature (see Kosegarten et al., 1997), subsequently stimulating proton pumping out of the cell. In fact, NH_4^+ uptake alkalinizes the cytoplasmic medium, while the ion's assimilation per se is proton neutral (Britto and Kronzucker, 2005). More importantly, as earlier in the book (see chapter 3), the authors fail to convey correctly how little charge has to move across a membrane before the membrane potential reaches unsustainable values, i.e., long before a change in cytoplasmic pH could be effected by transported and assimilated NH_4^+, compensatory ATPasedriven proton pumping must occur (effectively operating as an NH_4^+/H^+ antiport). Thankfully, the authors do not push the widespread dogma of passive NH_3 penetration as the normal means of uptake. However, they neglect to discuss recent findings of exceptional influx and efflux rates for NH_4^+ in the low-affinity range, and associated fundamental insights (see Britto et al., 2001). This is perplexing, because a specific, seemingly universal, comment is made that NH_4^+ efflux constitutes a ''small fraction of influx'' (p. 189). The discussion of NO_3^- uptake is less problematic, although the authors present an incorrect chemical equation for nitrate reduction (p. 181, eq. 7.2), where mystery electrons become involved in the process (the equation is not redox-balanced). Redox issues also plague the equation for nitrite reduction (p. 182, eq. 7.3), and the claim of a redox state of –IV for sulphur: such a state does not exist under reasonable chemical conditions. Clearly, this chapter would have benefited from more attention to chemical and transport detail, and editorial care, and, as such, is not of the caliber of other chapters in the book.

Chapter 8: Mineral metabolism—This chapter may be seen as ''mineral elements, part II.'' Essentially, it is an expansion of chapter 3. The treatise here is not dissimilar to the approaches in Marschner (1995) and Mengel and Kirkby (2001), although, again, with more attractive diagrams (as seen, e.g., in the fine illustration of zinc fingers). Generally good, if succinct, tie-ins are made with major physiological roles of the nutrients under discussion, and it is a minor point that proper physiological charge states are shown for some compounds (e.g., pyruvate) but not for others (e.g., phosphate and pyrophosphate). The section that stands out here is the one on silicon. Silicon is often ignored in nutritional discussions, and few authors would be more qualified than Epstein to present a synopsis.

Chapter 9: Nutrition and growth—The chapter begins with a discussion of nutritional seed reserves, with good comparative data on various kinds of seeds and seed compounds, and a successful effort is made, as elsewhere in the book, to relate plant nutrition to human nutrition. Excellent examples are given to illustrate the powerful, and to some extent obvious, link between plant nutrient absorption and plant development, in particular root development. Nitrogen, osmotic, and pH effects receive attention, and a discussion emerges of differential absorption in various parts of the roots system and of the variability of internal resource allocation between plant organs. This is followed by thoughts on nutrient regulation, the functional equilibrium that ensues from, or manifests itself in, ''plant demand,'' and even issues of seasonality are discussed. A more agronomic section fittingly follows, providing a good introduction into the sigmoidal relationship between photosynthesis and leaf nitrogen, and a definition of nutrient use efficiency. The authors avoid the multiplicity of definitions of use efficiencies and make a decision for the reader. In addition, they provide an excellent brief discussion of major trends in crop breeding vis-à-vis nutrient supply and of crop nutrient analysis. A useful chapter.

Chapter 10: Physiological genetics and molecular biology—This forms the introduction to the book's final section, ''Heredity & Environment.'' It begins with an area where Bloom possesses outstanding expertise, the commonalities and differences between wild and domesticated species. The authors include the well-known anecdote about a group of people searching for a lost key in the dark, solely under a streetlight, to illustrate fundamental issues with human endeavors in science—a mild, yet powerful, sidekick is administered here to the current plant biology focus on *Arabidopsis*, often to the exclusion of other species, and the dangers of extrapolation. The authors then provide a very rapid synopsis of major molecular advances of late in the identification of specific nutrient transporters. Slightly more expanded sections are provided on proton pumps (accompanied by instructive phylogenies) and potassium transporters (largely similar to the summary by Mäser et al., 2001), and shorter sections on calcium, sodium, ammonium, nitrate, phosphate, sulfate, and heavy-metal transporters as well as aquaporins (here, a brief discussion of important recent developments on the more general role of aquaporin-type transporters in transmembrane trafficking of uncharged molecular species, such as ammonia, would have been topical and useful; see Jahn et al., 2004). The authors largely bypass an opportunity to discuss salinity tolerance breakthroughs (even though key papers are cited, and the authors return to the subject later), the problems associated with heterologous expression systems, which have formed the basis of most functional characterizations of transporters, and the evolutionary aspects of transporter multiplicity. Nevertheless, the chapter provides a serviceable introduction into molecular advances in this field.

Chapter 11: Ecology and environmental stress—Very broad questions are asked here, and the authors' effort to integrate plant nutrition into this larger context is admirable. One gets the impression, however, of a ''blitzkrieg'' discussion, with an attempt at the summary of the science of ecology and of evolutionary theory in perhaps not the right place. A more colloquial writing style also emerges here, evident in, for instance, the quotation of Bob Dylan lyrics in the context of wind dispersal of plant seeds and fruits, and elsewhere. This in itself is not a failing, but seems incongruent with other parts of the book. Nevertheless, issues of habitat and phenotypic plasticity are linked well, and nutrient accessibility and heterogeneity, and growth habit appropriately re-enter the picture in this chapter. Here also a discussion of mycorrhizal associations finally occurs. The authors do a good job emphasizing the variable and highly nutrient-dependent contribution of mycorrhizal fungi to plant nutrition, rather than espousing the more dogmatic view assumed by some prominent workers in the mycorrhizal field that most, if not all, nutrient absorption occurs via the fungal component of the symbiosis. Too general, however, is the coverage of environmental stressors—chilling, heat, drought, flooding, salinity, and heavy metal exposure—are traveled through with incredible speed, and more detail would have been helpful. The authors criticize the widespread use of the term ''stress'' in biology, but their criticism, while certainly not unfounded, is also not especially necessary or productive. In general, this chapter has its merits, but its sweeping, and at times pedantic, overtones detract from thorough enjoyment and intellectual gain.

Chapter 12: Big picture: past, present, and future—Here, the authors go even further than in the previous chapter and ambitiously discuss ''A brief history of the world.'' Whether this is appropriate in a plant nutrition book is a question of taste, but it makes for a nice platform for grander afterthoughts to the main treatise. The facts on the origin of life do not take into consideration the recent questioning of the Warrawoona fossils of Western Australia by Prof. Brasier of Oxford University (Brasier et al., 2002) and others, and, as such, are not as up-to-date as one would hope. However, the timeline of plant evolution is presented succinctly and well, as is the discussion of Lovelock's Gaia hypothesis and the major issues of atmospheric change and recent alterations in biogeochemical cycles. As the authors point out rather correctly, speculations about the future have a tendency to age ungracefully, and, thus, not too large an effort is made to predict what contributions the science of plant nutrition may make to these global issues. Instead, what is offered is conservative and solid, and the focus of some recent successes in particular in the engineering of salinity-tolerant crop plants by E. Blumwald and co-workers (see Blumwald, 2003, for a recent review) is a fitting way to finish the expedition into what plant nutrition can accomplish and what kinds of approaches will likely govern the discipline in the coming years.

In summary, the treatise by Epstein and Bloom is well worth the acquisition. It rises to the difficult task of summarizing a vast, almost unmanageable discipline in a comprehensive way, while making it an interesting, and at times fascinating, read. It is recommended not only to experts in the field, but also to any plant biologist of today. Their contribution is ambitious and personal, and stands well alongside other, more classical, treatises of plant nutrition, although it is not as easily used as one's only reference of plant nutrition. An apt recommendation would be to use the book as part of a triad of plant nutrition works that includes Marschner (1995) and Mengel and Kirkby (2001), as a supplemental, more modern, resource. In an endeavor of this proportion, it is not surprising that some errors and omissions occur, and, if the reader is aware of where the major shortcomings lie, Epstein and Bloom's new edition must be seen as a strong and enjoyable addition to the fundamental library of plant nutrition.

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