Introduction

Plants require 17 chemical elements in order to complete their life cycles. These 17 elements are divided into major groups, the macronutrient elements and the micronutrient elements. The nine macronutrient elements are C, H, O, N, K, P, Ca, Mg and S, and the eight micronutrient elements are Fe, Mn, B, Zn, Cu, Cl, Mo and Ni (Marschner, 1995). Plants require greater quantities of the macronutrient elements than the micronutrient elements. Micronutrient elements are often called trace elements because they are needed in small quantities. There are also beneficial elements required by some, but not all species, and these elements include Si, Na, Co, and Cr (Marschner, 1995). All of these essential and beneficial elements are considered in formulating nutrient solutions or fertilizers for plant growth and development. Some of the chemical elements discussed below are components of macromolecules that are in important plant structures like cell walls. Other chemical elements may be found within the structures of enzymes called metalloenzymes, and others may be involved in activation of enzymes. Those chemical elements used in enzyme activation are required in much larger quantities than those required for metalloenzymes. However, it should not be surprising that there are many variations in the quantities of individual chemical elements needed by specific plants. In 2009, so much is known about plant structure and metabolism that one can explain many of the differences in nutrient element requirements of specific plants. As we move toward more efficient use of nutrients, it will be important to think about the unique structures and physiology of crop plants when considering their nutrient requirements and associated management.

Why do some plants have high potassium requirements?

Potassium is a small, univalent cation that is not toxic in plant cells even at rather high concentrations. Healthy plant cells contain high concentrations of K, but the question is why? What does K do inside the plant? The reason we have these questions about plant K may be because K is small and very mobile in plant cells, making it difficult to pin point its exact roles. The cytoplasm in most healthy plant cells contains over 100 mM K. This is precisely the K concentration needed to promote protein synthesis (Fig. 1; Blevins, 1985). Every

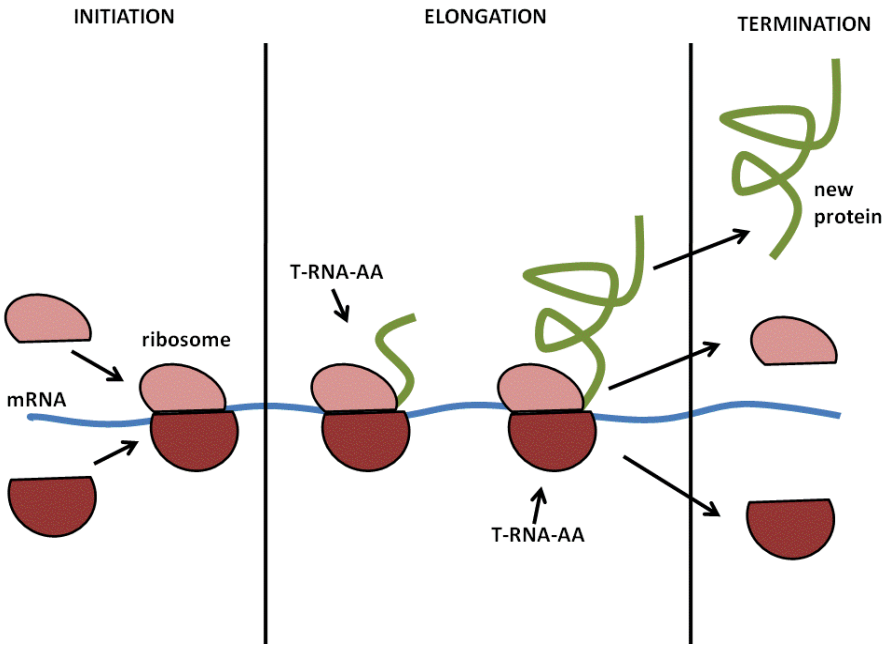

Figure 1. Each major step in protein synthesis must be bathed in >100 mM K. Ribosome subunits join along the messenger RNA (mRNA), and travel forward reading the code for additions of specific amino acids (AA) to the new protein chain. Each amino acid is carried in by a transfer RNA (t-RNA).

step of protein synthesis requires over 100 mM K for all of the structures involved to form the correct conformations necessary in the process. Correct structures are extremely important for the interactions of m-RNA, t-RNA, small ribosomes, large ribosomes, and the elongating protein. These structures must have the proper conformations in order to come together and then break apart at the right time. The conformations of these structures and their appropriate activities are only correct when they are bathed in high K concentrations. Similar concentrations of other monovalent cations do not produce the proper conformations. There are over 60 important enzymes that require K-activation in order to reach their maximum catalytic activity, and major processes like protein synthesis and starch synthesis involve some of these enzymes (Evans and Sorger, 1966).

Interestingly, certain plant species are known for their high K requirements. For example, alfalfa crops has a high K requirement for maximum productivity, removing about 42 lbs K in each ton of hay harvested. In trying to determine the reason for this high K requirement, I considered sugar, starch, protein, and oil production of different crops and compared these factors with K removed by the crop (Fig. 2 left; Blevins, 1985). The only factor highly correlated with K removal was protein removal, supporting the connection between K and protein synthesis discussed above. In fact, this correlation was also high when K and protein contents of grain crops were compared (Fig. 2 right). Therefore, if one is growing a crop that produces large quantities of protein/acre, the K requirement will be high. In addition, the cation, K^+, is required to balance the negative charges of the acidic amino acids, aspartate and glutamate, that extend out from the amino acid polymers. Therefore, there are two important reasons why high protein crops require large quantities of K.

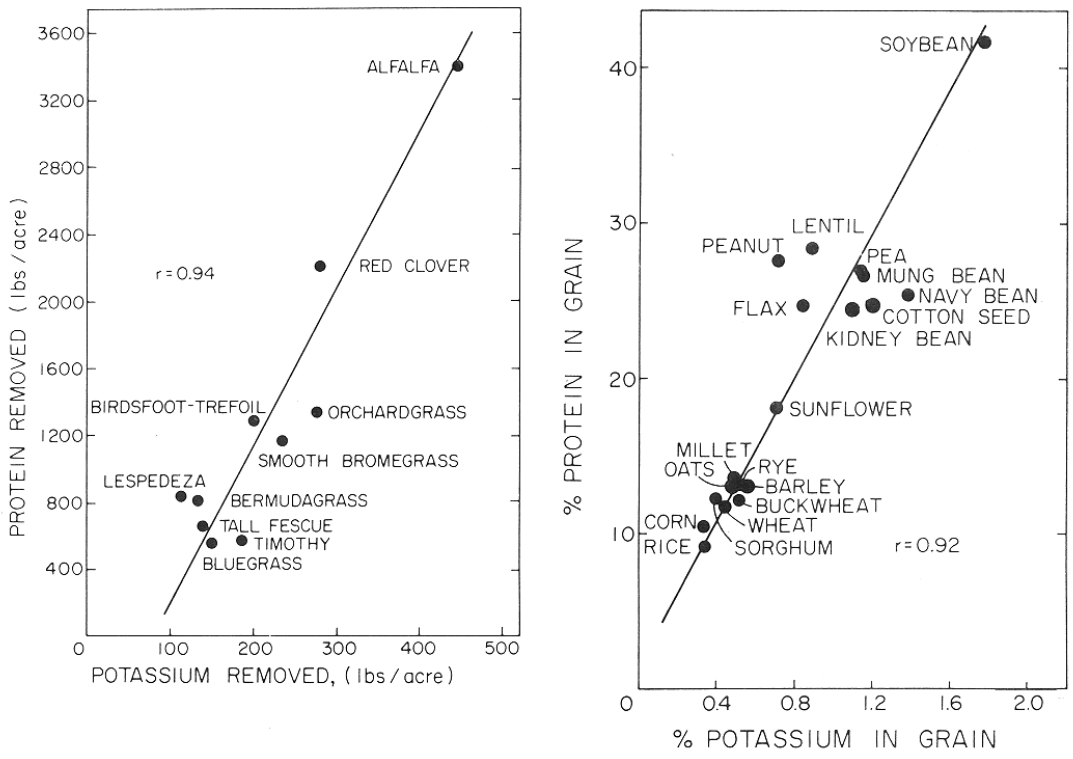

Figure 2. Potassium removed compared to protein removed when harvesting forage crops (left) and potassium content compared to protein content of grains (right) (Blevins, 1985).

Why do boron requirements differ among plant species?

Boron is an important micronutrient element required for all plant species. Interestingly, plants can be divided into four categories based on the quantity of B required: 1) Lactifers, contain the highest amount of B (70-100 ppm); 2) Cole crops (Brassica) have the second highest B concentrations; 3) Legumes and the lily family of monocots are in the third group and 4) Graminaceous plants (the grasses) contain the least amount of B (2–5 ppm) (Blevins and Lukaszewski, 1998). When graminaceous plants flower, their B requirements increase. Now we know that, except for the lactifers, the B content of plants is closely aligned with the amount of pectin in their cell walls (Hu et al, 1996). Cell wall scientists have discovered that the RGII (rhamnogalacturonan-II) fraction of cell wall pectin contains B, and that cell wall structures in plants differ among species (Fig. 3; Blevins and Lukaszewski, 1998). Grass plants have very different cell walls compared to other species. Cell walls of grasses are much lower in pectin, and therefore these plants contain less B (Hu et al, 1996).

Why do some plant species have higher manganese requirements than other species?

NAD-malic enzyme C4 plants – Plants that use C4 photosynthesis pathways have greater photosynthetic efficiency in high light conditions than C3 plants and, in general, have greater N-, P- and K-use efficiencies (Buchanan et al, 2000). This means that C4 plants produce more dry matter per unit of N, P or K than most C3 plants under high light conditions.

Although there are several sub-types of C4 plants, these are generally split into three main categories based on enzymes used to release CO_2 in bundle sheath cells (Fig. 4). The three enzymes are: 1) NADP-malic enzyme, or 2) NAD-malic enzyme, or 3) PEP carboxykinase (Table 1; Buchanan et al, 2000). The NAD-malic enzyme has an absolute requirement for Mn, while NADP-malic enzyme does not, and PEP carboxykinase can use either Mn or Mg (Burnell, 1988; Hatch and Kagawa, 1974). Corn and sorghum are NADP-malic enzyme sub-types, while millet, amaranth, Bermuda grass and switchgrass are Mn-activated NAD-malic enzyme sub-types (Table 2; Buchanan et al, 2000, Kering, 2008).

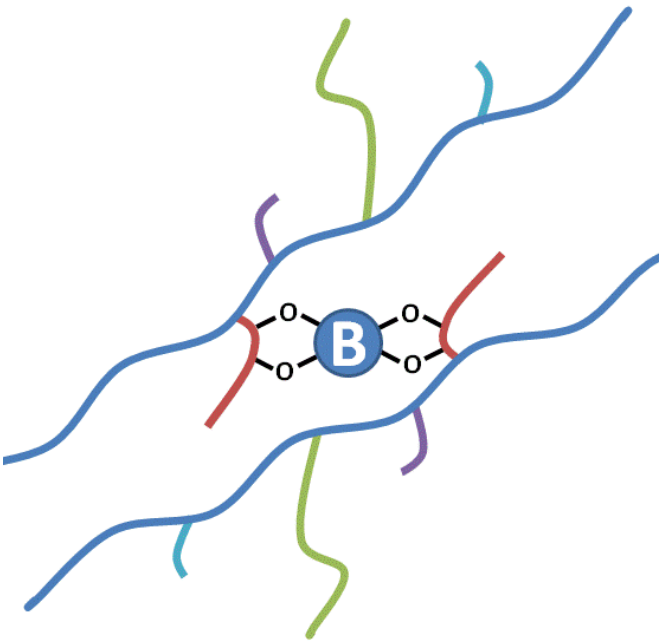

Figure 3. Boron as a structural component of cell wall pectin.

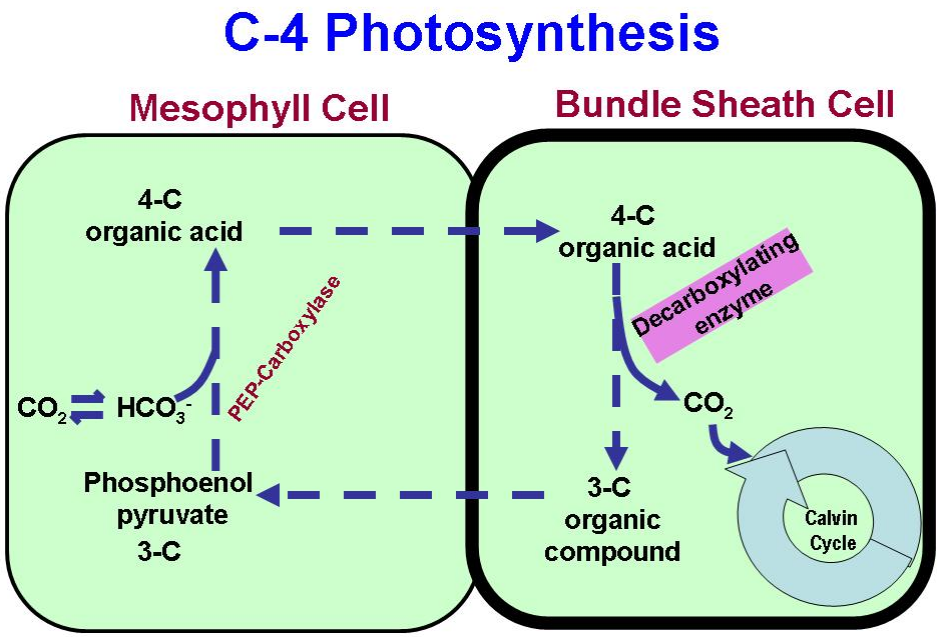

Figure 4. The carbon fixation and decarboxylation reactions of C4 plants (from Kering, 2008).

Table 1. The decarboxylating enzymes in different sub-types of C4 plants (from Kering, 2008).

• NADP-malic enzyme (NADP-ME)	(Mg activated)
• Phosphoenol pyruvate carboxykinase (PEP-CK)	(mainly Mn, Mg)
• NAD-malic enzyme (NAD-ME) ★	(Mn activated)

Table 2. Plant species in each of the three major C4 sub-types (from Kering, 2008). Species in boxes were used in experiments discussed below.

NADP-ME	NAD-ME	PEP-CK
Big bluestem	Pearl millet	Guinea grass
Indian grass	Amaranth	Rhode grass
Little bluestem	Bermuda grass	Side oats gamma
Crab grass	Switch grass	
Corn	Buffalo grass	
Sorghum	Blue gamma	
Sugar cane		

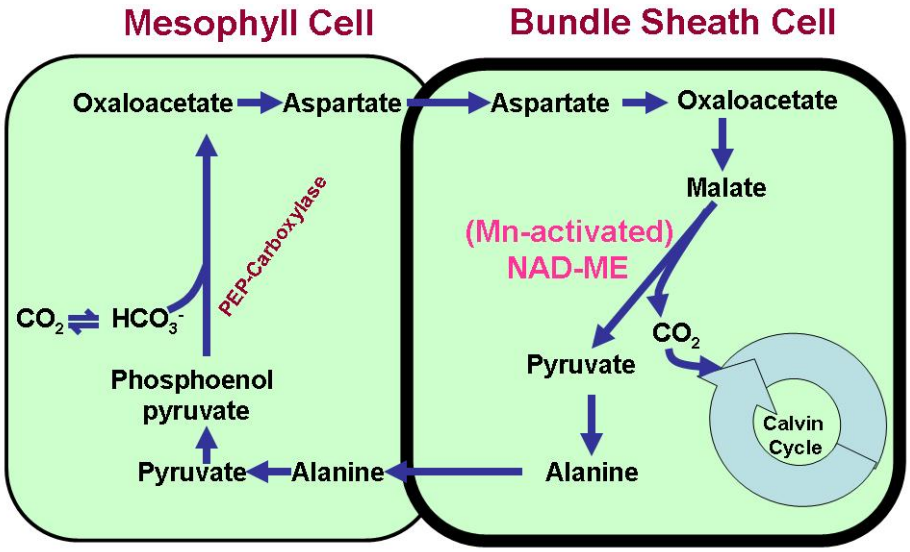

Figure 5. The Mn-activated NAD-malic enzyme releasing CO_2 in bundle sheath cell for Rubisco and Calvin cycle photosynthesis reactions (from Kering, 2008).

Since each carbon fixed in photosynthesis is released to the Calvin cycle in bundle sheath cells by Mn-activated NAD-malic enzyme in this sub-type of C4 plant, perhaps the Mn requirement of these plants would be higher than that of C3 or NADP-malic enzyme plants (Fig. 5). We tested this hypothesis by using hydroponic solutions where Mn concentrations could be carefully controlled. A survey of plant nutrient solution recipes indicated that most nutrient solutions contain around 2µM Mn. In this experiment, we compared the growth and photosynthetic rates of two NAD-malic enzyme C4 plants, Pearl millet and amaranthus, with two NADP-malic enzyme C4 plants, corn and sorghum, and two C3 plants, squash and wheat.

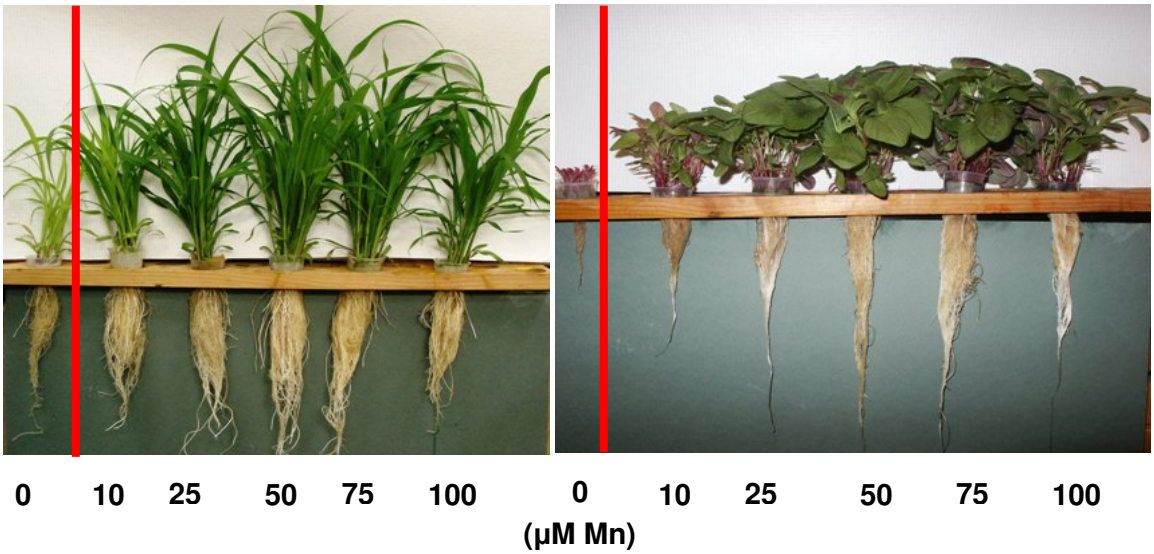

Figure 6. Root and shoot growth of Pearl millet (left) and purple amaranth (right) in hydroponic solutions containing increasing Mn concentrations (from Kering, 2008). Red lines indicate the Mn concentrations found in most plant nutrient solutions.

Corn, sorghum, squash and wheat produced maximum biomass with the normal 2 μM Mn concentration in the hydroponic medium (Kering, 2008; Kering et al., 2009). On the other hand, NAD-malic enzyme C4 plants, Pearl millet and amaranthus, produced maximum biomass with ~50 μM Mn in the nutrient solution (Fig. 6). Photosynthetic rate responses of each species to nutrient solution Mn concentration were similar to their biomass responses. These results clearly show that when all of the carbon going into photosynthesis goes through a single Mn-activated enzyme, plant growth response is dependent on high levels of available Mn.

Ureide-transport in leguminous plants and Mn requirements – Legumes are some of the highest protein crops grown, and they utilize N from the atmosphere rather that relying on N fertilizer to produce this protein. There are two major types of leguminous plants when it comes to root nodules and forms of N transported from these nodules to leaves and developing pods (Sprent, 1984). There are determinate nodules, which tend to be round, with life spans of about 35 days. These are nodules formed on roots of warm season legumes and contain bacteroids that fix atmospheric N and use the fixed N to synthesize the ureide molecule, allantoate, for transport in xylem to leaves and developing pods. Allantoate contains 4N's and 4C's, and is a very efficient molecule for transporting N. Cool season legumes have indeterminate nodules that are elongated and often form a Y-shape. Bacteroids in these nodules fix N and, in general, synthesize the amide, asparagine, for transport in xylem to leaves and pods. Asparagine contains 2N's and 4N's.

The fixed-N is released in leaves and developing pods of ureide-transporting legumes by an enzyme called allantoate amidohydrolase, and one interesting feature of this enzyme is that it is activated by Mn (Fig. 7; Lukaszewski, et al. 1992; Todd, et al, 2006; Winkler, et al, 1985, 1988). Therefore, according to the soil N status, a large proportion of the total N, mostly protein-N in the harvested legume, comes through this Mn-activated enzyme. As with the Mn-activated NAD-malic enzyme plants, perhaps ureide-utilizing leguminous plants, like soybean, cowpea and lespedeza, will require higher Mn nutritional levels than asparagine-transporting legumes, like alfalfa and clover or all legumes grown on nitrate-N. To my knowledge, the Mn-requirements of ureide-transporting, amide-transporting and nitrate-fed leguminous plants have not be directly compared.

In addition to a Mn-ureide metabolism connection, there is a Mn-bacteroid connection inside the root nodule. Bacteroids depend on their host legume for a source of energy (carbon) to support the nitrogen fixation process. Although plants usually transport sucrose via the phloem from leaves to root nodules, root nodule cells metabolize the sucrose and provide bacteroids organic acids, like malate, as an energy source. Bacteroids in nodules of some species, like soybean, use the Mn-activated NAD-malic enzyme in the initial step of malate utilization (Chen, et al, 1998). Therefore, a Mn-enzyme plays a central role in root nodule/legume N metabolism!

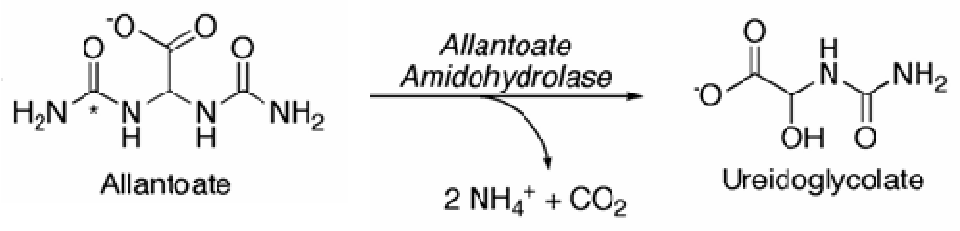

Figure 7. The reaction in ureide metabolism in leaves and developing pods of nitrogen-fixing soybeans featuring allantoate amidohydrolase, a **Mn-activated** enzyme.

Summary
The knowledge gained on structure and metabolism of a wide range of plant species over the past few years allows us to predict special nutrient needs. High protein plants require large quantities of K because components involved in protein synthesis must be bathed in high K concentrations in order to maintain the proper configurations. Plus, K^+ is used to balance the negative charges of asparagine and glutamine in proteins produced. Plants with pectin-rich cell walls have high B contents, and thus plants with low pectin cell walls have low B contents. NAD-malic enzyme sub-type C4 plants have high Mn requirements for maximum growth and photosynthesis rates since every C fixed is released in bundle sheath cells by this Mn-activated enzyme. Based on their ureide metabolism with the Mn-activated enzyme, allantoate amidohydrolase, and with malate as the primary C source for bacteroids via NAD-malic enzyme, N-fixing soybeans may have a higher Mn requirement than nitrate-N grown plants. In addition to these examples, there are other specific nutrient requirements that can be predicted based on our knowledge of plant structure and metabolism.

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