NEW AG INTERNATIONAL

A Closer and Fresh look at Potassium and Magnesium Roles:

TO FEED THE PLANTS OF COURSE BUT ALSO TO SAVE WATER

The role of magnesium in plant nutrition and productivity has been often underestimated particularly with respect to drought stress tolerance of crop plants and better seed and root formation. Potassium nutrition also impacts on growth and productivity of plants. Adequate and balanced fertilization with these two important nutrients helps to significantly increase the water use efficiency and drought stress tolerance of crop plants. During the reproductive growth stage of plants the demand for magnesium and potassium is particularly high to help and maintain extensive transport of carbohydrates into seeds (and roots/ tubers) and to alleviate photo-oxidative damage. Crop plants are usually exposed to high radiation (sunshine) and water deficiency during the reproductive growth stage which results in a higher physiological demand for magnesium and potassium. Late season foliar applications of magnesium and potassium fertilizers would, therefore, be a very beneficial and useful practice to contribute to better productivity and higher drought stress tolerance.

Based on the latest research compiled and developed by Prof Ismail Cakmak of Sabanci University (Turkey) with Prof Andreas Gransee, Head of R&D Agriculture at K+S KALI (Germany), New Ag International has the story.

TWO ESSENTIAL PLANT NUTRIENTS

MAGNESIUM nutrition of crop plants is very often overlooked, forgotten or underestimated in practical agriculture. Even in research programmes, magnesium does not receive as much attention as other mineral nutrients like nitrogen, phosphorus or potassium. However, the importance of magnesium in plant nutrition is reflected by its exceptional physiological functions and actions in plant cells. Any visible or hidden deficiency of magnesium can cause serious impairments in crop productivity and also nutritional quality.

Magnesium deficiency is becoming an important issue in arable farming, particularly in highly weathered acid soils, light and sandy soils and under intensive crop production systems. In practice, magnesium removal through high-yield cultivars is rarely balanced by application of fertilizers. For example, sugarbeets may remove up to 100kg magnesium from soil per hectare, but average fertilization stays below this level. Thus, intensification of crop production results in rapid depletion of magnesium in soils.

Also, soils over-fertilized with potassium and rich in soluble calcium are associated with high risk of magnesium deficiency. Published reports show that high application rates of potassium fertilizers in some locations in China cause development of magnesium deficiency in plants (Römheld and Kirkby, 2010, Plant Soil, 335: 155-180). Liming of acid soils with calcitic limestone represents a further factor which aggravates the magnesium deficiency problem in plants.

For optimal growth plants need to accumulate magnesium in the dry matter in a range between 0.2-0.5%. Magnesium is highly mobile within the plant. This is why deficiency symptoms occur on older leaves. Under deficiency conditions the magnesium is steadily retranslocated to younger parts of the plant. In soil solution, magnesium may occur in very high concentrations, as it is very mobile and soluble. Thus, there is a high risk of magnesium deficiency due to leaching into deeper, non-rooted soil layers.

Compared to magnesium, potassium is required in about 10-fold higher concentrations in the dry matter of crops. In contrast to this high demand, the concentration of potassium in the soil solution and its mobility is much lower than that of magnesium. Potassium is generally strongly bound to soil particles. The nature of the binding of potassium in the soil (e.g., exchangeable and fixed K) decides on the availability of the soil potassium to plants. Crops have developed adaptive mechanisms facilitating the access to these different soil potassium fractions. For instance, potassium uptake by plants is closely related to root growth and formation of root hairs. Better root growth and development gives access to new exchangeable soil potassium fractions and therefore contribute to constant ´re-supply´ throughout the growth period. Once taken up, potassium is, like magnesium, highly mobile within the plants so that deficiency symptoms first appear on older leaves. Potassium has also several important functions in plants cells including photosynthesis, translocation of photoassimilates, controlling the water regime of cells, protein synthesis and mitigation of the adverse effects of environmental stress factors, especially drought.

DROUGHT STRESS: THE MOST IMPORTANT ABIOTIC FACTOR

Drought represents the most important abiotic stress factor limiting crop production globally. It is expected that climate changes will cause more intense drought conditions, especially in combination with heat and high radiation stress. It is very obvious that the food production conditions will be more adverse and risky to meet the food demand of the increasing world population. According to FAO estimates, water deficiency is and will be one of the most important limiting resources in agricultural production.

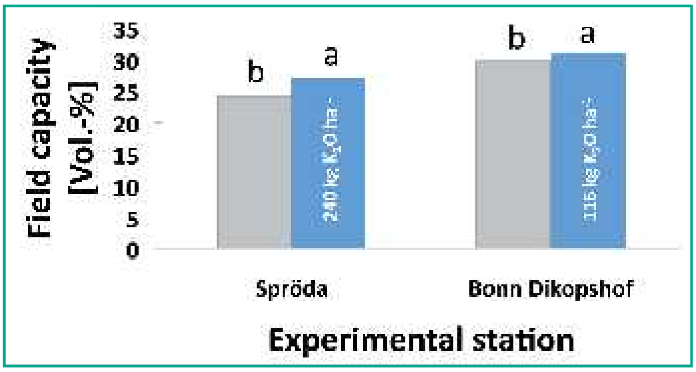

Figure 1: Effect of K fertilization on the field capacity of a light (Spröda) and heavy (Zatec) soil (modified after Holthusen, 2010).

In order to meet the increasing world food demand under adverse food production conditions, different types of agronomic strategies are required to improve drought stress tolerance and water use efficiency of crop plants. Among the agronomic factors contributing to better yield under drought stress, mineral nutritional status of crop plants and nutrient management practices (e.g., fertilization) play a critical role. Increasing evidence is available showing that plant nutrients like magnesium (Mg) and potassium (K) play important roles in alleviating drought stress by influencing important metabolic processes and thus water use efficiency. Water use efficiency expresses the amount of yield produced per unit of water.

As already stated, various key physiological processes in plants are substantially affected by potassium and magnesium nutrition of plants. Deficiency of one or both of these nutrients vitally impairs plant growth and development and increases the susceptibility to biotic and abiotic stresses like drought stress.

INCREASING THE USABLE FIELD CAPACITY

The expression ´field capacity´ describes the capability of a soil to keep water against gravity. The plant available part of this soil water amount is called usable field capacity. Recent results of long-term field trials on light and heavy soils showed a positive impact of potassium fertilization on field capacity. As shown in Fig. 1, potassium fertilization was effective in improving the field capacity by about 2-3% compared to soils where potassium fertilization was omitted for a longer period. This impact of potassium fertilization on available water holding capacity of soils would be of great importance for crop plants growing under drought stress conditions.

How can this positive effect of potassium fertilization on usable field capacity be explained? The usable field capacity is greatly determined by the pore size distribution. Medium-sized pores are particularly important. If pores are too small, the water is bound quickly and firmly, and is therefore not available to plant roots. Large pores are not able to keep the water, thus allowing it to quickly drain off into deeper soil layers (situation displayed on the left of Figure 2). Potassium facilitates the formation of "bridges" (e.g., between clay minerals and potassium), dividing large pores into medium pores, which are more effective in keeping water against gravity, thus keeping it available for roots. This is a specific effect mediated by potassium ions in soils (situation displayed on the right of Figure 2).

MAINTAINING CARBOHYDRATE FORMATION AND PARTITIONING

Photosynthesis is the fundamental process in plants. It provides carbohydrates and energy for growth and development. For photosynthesis both magnesium and potassium are essential elements. First, the need for magnesium in photosynthesis is reflected by its role as central atom in the chlorophyll molecule (Fig.3). Moreo-

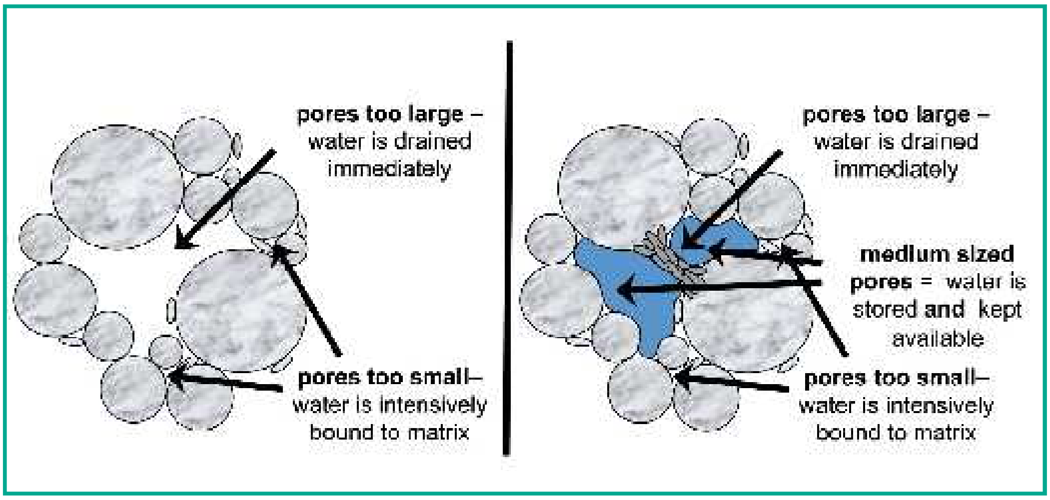

Figure 2: Schematic image of the role of potassium in increasing the usable field capacity of soils by forming medium sized pores through bridge formation between soil particles.

ver, a fine-tuned pH regulation is needed because photosynthetic enzymes need specific pH to work properly. For instance, this is true for ribulose-1,5-bisphosphate (RuBP) carboxylase as key enzyme in photosynthetic carbon fixation. Magnesium and potassium help to build up a pH gradient across chloroplastic membranes which is required for the formation of ATP (Adenosine triphosphate, the universal energy equivalent) through photophosphorylation (Marschner, 2011, Mineral Nutrition of Higher Plants, Academic Press).

Both magnesium and potassium are needed not only for biosynthesis of photoassimilates (photosynthates) but also for their translocation into growing parts of plants via phloem, such as into seeds or grains, roots and tubers. This source-to-sink transport of metabolites, e.g. sugars derived from photosynthesis, starts with phloem loading and subsequent mass flow-driven solute transport. Potassium is important for both parts; it is involved in (i) maintaining a high pH in the sieve tube, a prerequisite for phloem loading, and (ii) helps to build up the osmotic potential in the sieve tubes, the driving force solute transport via mass flow (Marschner, 2011, Mineral Nutrition of Higher Plants, Academic Press). New results highlight the importance of potassium in phloem loading particularly under energy-limiting conditions which can temporarily occur in plants due to physiological or environmental factors (Gajdanowicz et al., 2011, PNAS). Phloem loading of sucrose is an energy consuming process involving the work of so-called H+-ATPases, which build up electrochemical gradients facilitating sucrose influx into the phloem (see also following section). Under low-energy conditions, where the H+-ATPase-driven formation of an electrochemical gradient may be hampered, the existing K gradient can serve as energy provision mechanism for phloem loading.

Published data indicate that phloem loading and transport of photosynthates are seriously impaired by magnesium deficiency. Consequently, in magnesium-deficient plants there is a massive accumulation of carbohydrates (e.g., sucrose) in source leaves while the concentration of sucrose in phloem sap is very low (Fig.4). The depressive effect of low magnesium supply on phloem transport of sucrose is specific, and occurs very early before any clear change in chlorophyll amount, photosynthesis rate or shoot growth takes place (Cakmak et al., 1994, J. Experimental Botany). The distinct role of magnesium in phloem transport of photosynthates has been shown in a number of crop plants (Hermans et al., 2006, Trends in Pant Sciences; Cakmak and Kirkby, 2008, Physiol. Plant.). There is no direct experimental evidence about how and why magnesium affects phloem export of sucrose. One plausible explanation is related to the dependency of the phloem loading process to Mg-ATP that is used by H+-ATPase enzyme (see above). Low concentration of Mg-ATP in the phloem loading sites can be one major reason for impaired phloem transport of sucrose in magnesium-deficient plants. A resupply of magnesium to magnesium-deficient plants for only one day is very effective in restoration of the phloem transport of sucrose (Cakmak and Kirkby, 2008, Physiol. Plant). These results clearly indicate fundamental roles of magnesium and potassium in phloem export of photosynthates.

What are the consequences of impaired photoassimilate partitioning, and how does this affect water use efficiency? Due to marked inhibitions in transportation of photoassimilates into roots, root growth is seriously affected by both magnesium and potassium deficiency stress. For a high water use efficiency plants need a sufficiently developed root system to continuously get access to water, even under drought stress conditions. Results available in literature show that both magnesium and potassium deficiencies results in drastic inhibitions in root growth before causing any obvious change in shoot growth and chlorophyll concentration (see Fig. 5). Such early and substantial impairments in dry matter allocation into roots lead to high shoot to root dry weight ratios. In literature it is well known that impairments in root growth (e.g., rooting depth, root length etc) are associated with reduced water use efficiency of crop plants. Rapid decreases in root growth as a consequence of magnesium and potassium deficiencies may vitally reduce uptake of water and mineral nutrients from the soil. This effect could be of great importance in soils with a limited supply of water and nutrients.

INCREASING THE TOLERANCE TO DROUGHT STRESS

Nutritional status of plants with magnesium and potassium is also important for drought stress tolerance. Use of absorbed light energy in photosynthetic carbon fixation is a critical issue under stress conditions. If the light energy absorbed and electrons released

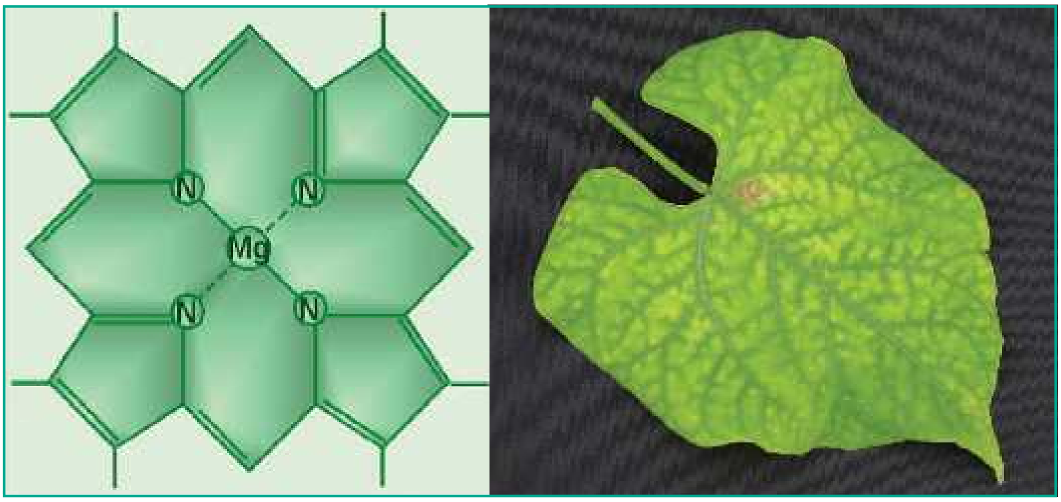

Figure 3: Magnesium: the central atom of the chlorophyll molecule (left). As a consequence magnesium deficiency symptoms are expressed as interveinal chlorosis (right).

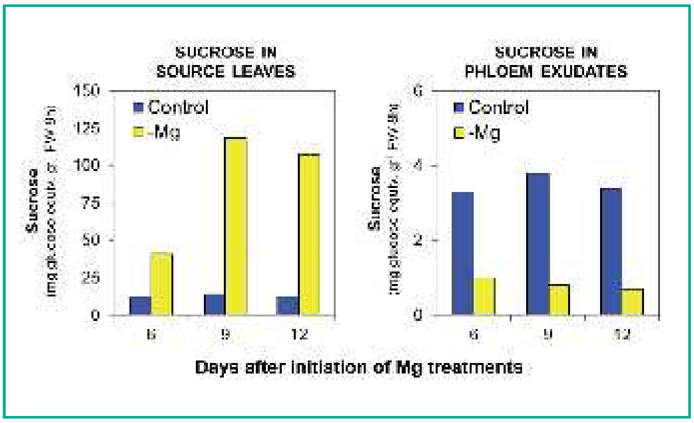

Figure 4: Effect of adequate (control) and low supply of Mg (designated as -Mg) on concentrations of sucrose in primary (source) leaves and in phloem exudates (phloem export from the source leaves) in common bean plants over 12 days of growth (redrawn from Cakmak et al 1994, J. Exp. Bot. 45: 1251-1257)

Figure 5: Effect of low and adequate (left) and increasing (right) Mg supply on shoot and root growth of wheat plants (Courtesy of Dr I. Cakmak)

are not used in photosynthetic carbon fixation in chloroplasts, for example due to drought stress or nutrient deficiency, this excess of energy and electrons is transferred to oxygen causing generation of highly toxic oxygen free radicals and resulting photooxidative damage in chloroplasts. This photooxidative damage is a common process in crop plants under drought stress, and stimulated by the factors which further limit photosynthetic carbon fixation such as potassium and magnesium deficiencies (Cakmak, 2005, J. Plant Nutr. Soil Sci.; Cakmak and Kirkby, 2008, Physiol. Plant). Several reports are available in literature showing that adequate potassium nutrition alleviates drought damage in plants by mitigating photooxidative damage in plants under water limited conditions (see Römheld and Kirkby, 2010, Plant and Soil and Cakmak, 2005, J. Plant Nutr. Soil Sci.)

REGULATING THE WATER HOUSEHOLD OF PLANTS

Water flux takes place from locations of higher water potential to places with lower water potential. In the roots a sufficient potassium concentration is needed by the plant to build up such water potential gradients between the soil and the roots thus facilitating water influx. Another critical factor for improved water use efficiency is the function of the stomata, pores in the leaf epidermis which facilitate gas exchange between plant and atmosphere. Carbon dioxide (CO_2) diffusion into the leaf is crucial for photosynthesis. With respect to water use efficiency, stomatal water vapour exchange plays a key role as well. The water household of the plants is severely disturbed due to unrestricted and unproductive water loss due to insufficiently regulated stomatal closure. To reduce unproductive water loss, an adequate supply of potassium is necessary, since potassium is a key component for effective stomata movement (Fig. 6). Transport of potassium across the plasma membrane into the so-called guard cells causes turgor changes. These guard cells accumulate potassium, which reduces their water potential leading to osmosis-driven water uptake. The cells become turgid and stomata open for CO_2 diffusion into the leaves. By exporting the potassium back into the neighbouring cells the water flux is reversed and the stomata close. In addition to this specific function of potassium, the stomatal conductance was shown to be significantly reduced under magnesium deficiency.

It is very obvious that there are four major factors contributing to high water use efficiency and drought stress tolerance, which are under direct influence of magnesium and potassium fertilization: (i) increase of usable field capacity of soils through potassium-clay bridge formation, (ii) maintenance of formation and translocation of carbohydrates within the plant for an effective root growth and development, (iii) alleviation of photooxidative damage in chloroplasts under drought conditions by affecting utilization of absorbed light energy in photosynthesis and (iv) reduction of unproductive water loss through effective stomata regulation.

The latest research conducted on the subject brings further clear evidence of the specific role that some nutrients can play in water management strategies. ■

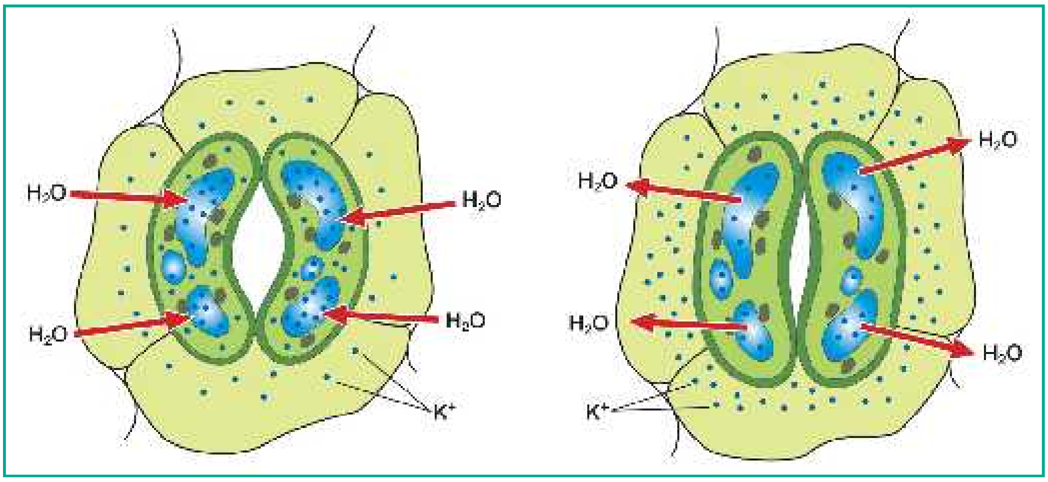

Figure 6: Schematic view on the role of potassium in stomata regulation, stomata opening (left) and stomata closure (right).From K+S KALI GmbH, publishing as Benjamin Cummings

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