Functioning of potassium and magnesium in photosynthesis, photosynthate translocation and photoprotection

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Potassium (K) and magnesium (Mg) are mineral nutrients that are required in large quantities by plants. Both elements critically contribute to the process of photosynthesis and the subsequent long-distance transport of photoassimilates. If K or Mg is not present in sufficient quantities in photosynthetic tissues, complex interactions of anatomical, physiological and biochemical responses result in a reduction of photosynthetic carbon assimilation. As a consequence, excessive production of reactive oxygen species causes photo-oxidation of the photosynthetic apparatus and causes an up-regulation of photoprotective mechanisms. In this article, we review the functioning of K and Mg in processes directly or indirectly associated with photosynthesis. Focus is given to chloroplast ultrastructure, light-dependent and -independent reactions of photosynthesis and the diffusion of CO₂ – a major substrate for photosynthesis – into chloroplasts. We further emphasize their contribution to phloem-loading and long-distance transport of photoassimilates and to the photoprotection of the photosynthetic apparatus.

Introduction

Almost all plant species on Earth are autotroph and produce complex carbon compounds by the process of photosynthesis in which solar energy is captured. The solar energy capture is the basis for productivity and the net amount of carbon which is photosynthetically assimilated in 1 year by the vegetation, the so called net primary production, is suggested to be 104.9 Pg (Field 1998) (1 Pg = 10¹⁵ g). The net primary production is considered the available amount of energy that can be transferred from plants to other levels of trophic webs in ecosystems (Haberl et al. 2007), e.g. human consumption of agricultural commodities. Agricultural production is suggested to grow by 60–100% in the next four decades (Krausmann et al. 2013), outlining the importance of photosynthesis and ensuing processes. For unabated photosynthesis, optimal conditions are required which include optimal nutrient supply. Potassium and magnesium are essential mineral plant nutrients that critically contribute to the process of photosynthesis and the subsequent long-distance transport of photoassimilates. Among the mineral nutrients, nitrogen (N) is generally required in the largest quantity by plants, followed by potassium (K), phosphorus (P), calcium (Ca) and magnesium (Mg). Plants take up both mineral Mg and K only in the cationic form (as Mg²⁺ and K⁺). High K concentrations in the soil solution inhibit Mg uptake and may induce Mg deficiency in plants (Salmon 1963, Heenan and Campbell 1981).

Within plants, most metabolically active Mg is bound or incorporated into cellular compartments (Waters 2011), with highest concentrations in chloroplasts (Karley and White 2009). A significant share of Mg in leaves is bound as the central atom in the tetrapyrole ring of chlorophyll a and b molecules, which are the major

Abbreviations – APX, ascorbate peroxidase; GR, glutathione reductase; LHCII, light harvesting complex II; NPQ, non-photochemical quenching; PPFD, photosynthetic photon flux density; PS, photosystem; Rca, Rubisco activase; ROS, reactive oxygen species; RuBP, ribulose-1,5-bisphosphate; SLM, specific leaf mass; SOD, Fe- and CuZn-superoxide dismutase.
pigments for photosynthetic light absorption (Wilkinson et al. 1990). In contrast, K is not part of organic macromolecules and exclusively present in its ionic form (K\(^{+}\)) or in weak complexes from which it is easily exchanged (Marschner 2012). In cells, K\(^{+}\) is present in two major pools, the vacuole and the cytosol. In the latter, K\(^{+}\) is the most abundant cation. K and Mg are both mutually involved in a number of physiological processes, including the activation of numerous enzymes and regulation of the cation-anion balance (Marschner 2012). K\(^{+}\) serves as the most important inorganic osmotic compound in plant cells, and thus, sufficient K supply is crucial for the regulation of turgor-driven processes like stomatal movement (Fischer 1968) and cell elongation (Mengel and Arneke 1982). K facilitates the diffusion of CO\(_2\) from the atmosphere into chloroplasts (Jákli et al. 2017). K and Mg are additionally involved into phloem-mediated sucrose transport and the distribution of photoassimilates within the plant.

Both K and Mg play prominent roles in processes that are tightly associated with photosynthesis and photosynthetic translocation (Fig. 1). So far, the role of K and Mg in photosynthesis and associated processes has not been covered in a comprehensive review. Many reviews focus on the movement of K or Mg within plants (Shaun 2002, Gierth and Mäser 2007, Britto and Kronzucker 2008, Szczesba et al. 2009), on the contribution of these elements (especially K) to stress alleviation (Cakmak 2005, Wang et al. 2013) or, in somewhat broader approaches, on their status in global agriculture (Römheld and Kirkby 2010, Cakmak et al. 2013, Gransee and Führs 2013, Zörb et al. 2014). Therefore, our main objective is to close this gap by providing a comprehensive overview of the processes that are affected, facilitated and regulated by Mg and K in photosynthesis, photoassimilate translocation and photoprotection.

We will first highlight the role of Mg and K in the light-independent and light-dependent photosynthetic processes including (1) CO\(_2\) diffusion through the leaf boundary layer, stomata and mesophyll, (2) chloroplast ultrastructure, (3) chlorophyll synthesis and (4) Rubisco activation and activity (Fig. 1A–D). Then, we will evaluate the role of Mg and K in photoassimilate translocation (Fig. 1E). Finally, we will highlight photoprotective responses, including non-photothermal quenching (NPQ), scavenging of reactive oxygen species (ROS), photorespiration, chloroplast movement and leaf movement.

**K and Mg involvement in photosynthesis**

Rates of photosynthetic CO\(_2\) assimilation are stable over a broad range of K and Mg concentrations within leaves. However, it has long been recognized that adequate K and Mg nutrition is required to maintain the photosynthetic activity of crops (e.g. Cooper et al. 1966, Terry and Ulrich 1973, Peoples and Koch 1979). Below a certain threshold of leaf K, assimilation rates drop drastically. The tissue K concentration that is critical for photosynthetic functioning of crops (i.e. the tissue K concentration where net assimilation is 95% of its maximum under experimental conditions) is reported between 12.5 and 14.0 mg Kg\(^{-1}\) dry matter in oilseed rape (Lu et al. 2016a), 13.0 mg g\(^{-1}\) in soybean (Singh and Reddy 2017), 22.3 mg g\(^{-1}\) in sunflower (Jákli et al. 2017) and 26.0 mg g\(^{-1}\) in cotton (Gerardeaux et al. 2010) (critical values for Singh and Reddy (2017), Jákli et al. (2017) and Gerardeaux et al. (2010) are calculated from the model equations presented in the respective publications describing the relationship between leaf K concentration and net assimilation). Critical leaf Mg concentrations for photosynthesis have not been reported, but concentrations of 0.7 mg g\(^{-1}\) leaf dry matter may be required to achieve 90% of maximum yield (Smith et al. 1985).

**Restrictions in CO\(_2\) diffusion**

In the light-independent photosynthetic reactions atmospheric CO\(_2\) is fixed via enzymatic carboxylation. The rate of CO\(_2\) fixation during this process not only depends on bio- and photochemical processes, but also on the quantity of CO\(_2\) that is available for Rubisco in the chloroplast stroma. A number of resistances restrict the diffusion of CO\(_2\) from the atmosphere into the leaf-internal airspace and further through cell wall, plasma membrane, cytosol, chloroplast envelope and stroma (Fig. 1A).

**Boundary layer diffusion**

The first resistance against CO\(_2\) movement from the atmosphere towards the leaf surface is posed by the leaf boundary layer. In this thin layer adjacent to the leaf surface, turbulent exchange is suppressed and the transfer of molecules is characterized by diffusion (Schuepp 1993). The thickness of the boundary layer, and thus its conductivity to CO\(_2\) diffusion, is determined by the leaf energy balance (Woodrow et al. 1990) rather than by biochemical parameters and is hence not likely to be directly influenced by leaf nutrient status. Therefore, it has been largely neglected in studies of nutrient effects on CO\(_2\) exchange. However, due to its osmotic properties, K deficiency causes a loss of turgor potential (Carroll et al. 1994), and this can substantially affect leaf inclination of plants. Boundary layer conductance is a function of both radiation interception and wind speed (Martin et al. 1999). A change in average leaf inclination under
conditions of K deficiency may therefore substantially affect boundary layer properties and thus change its conductivity to molecular diffusion, with effects on photosynthesis, transpiration and water-use efficiency (Collatz et al. 1991, Schuepp 1993, Bridge et al. 2013). This effect appears to be unique to K deficiency and is not likely to result from a deficiency of Mg, as Mg does not contribute to osmoregulation. We are, however, not aware of any study directly relating K or Mg nutrition to boundary layer conductance, but its general concept should be considered when transferring results from leaf chamber measurements – where boundary layer effects are largely avoided by strong air mixing – to the field.

**Stomatal conductance**

CO₂ enters the leaf through the stomatal pores. Their aperture is mediated by the stomatal guard cells, which pose the first actively regulated resistance to the movement of CO₂ into leaves. The important role of K⁺ for the regulation of stomatal guard cells and the efficiency of stomatal movement is well documented (Fischer 1968, Humble and Raschke 1971). K⁺ is the major inorganic osmolyte, driving the changes in guard cell turgor that are required for stomatal movement. Dynamic regulation of stomatal aperture requires large quantities of K⁺ to be rapidly exchanged between apoplast, cytosol and vacuoles of stomatal guard cells (Roelfsema and Hedrich 2002, Andrés et al. 2014). Transport of K⁺ through the plasma membrane of stomatal guard cells is mediated by voltage-gated inward-rectifying K⁺ channels, and is accompanied by influx of counter-ions (NO₃⁻, Cl⁻) and synthesis of malate in the cytosol. Increased concentrations of ions decrease the guard cell water potential and cause an influx of water. As a result, guard cell volume increases and the stomata open.
Due to the osmotic role of K in guard cell regulation, it is not surprising that stomatal conductance is frequently reported to decrease under K-deficient conditions (e.g. Terry and Ulrich 1973, Zhao et al. 2001, Jákli et al. 2017). Nevertheless, and regardless of the importance of K⁺ in guard cell regulation, changes in stomatal conductance do not limit photosynthesis predominantly, even when total leaf K concentrations are below the critical level for photosynthesis (Sen Gupta et al. 1989, Zhao et al. 2001, Jin et al. 2011). The contribution of stomatal limitations to the total limitation of photosynthesis was estimated at about 15% in sunflower (Jákli et al. 2017) and did not increase even under severe K deficiency. The fraction of stomatal limitation even decreased from 55 and 50% to 36 and 20%, respectively, in two varieties of K-deficient oilseed rape (Lu et al. 2016a).

There is evidence that the velocity with which stomata react to environmental or biochemical feedbacks is diminished in K-deficient alfalfa (Lindhauer 1983) and olive tree (Erel et al. 2013). Erel et al. (2013) suggested that a functional substitution of K⁺ by Na⁺ might be responsible for alternations in the velocity of stomatal movement in olive, since the transport of Na⁺ through cell membranes is slow compared to the transport of K⁺.

Some reports indicate that under combined K deficiency and water-limitation, stomatal control may be lost in perlite-grown sunflower and olive plants, resulting in an inhibition of drought-induced stomatal closure (Fournier et al. 2005, Arquero et al. 2006, Benlloch-González et al. 2008, 2010). In accordance with the general concept, the authors do not attribute their results to a loss of osmotic stomatal control, but to an inhibition of the ABA signaling pathway by excessive ethylene production in the leaves. These results are not supported by findings of Jákli et al. (2017), who reported decreased rates of stomatal conductance in K-deprived and PEG-stressed sunflower grown in nutrient solution, and Erel et al. (2013), who did not find any effect of K deficiency on stomatal conductance in drought-stressed, perlite-grown olive.

The origin of this contradiction remains speculative, and the interaction effect of K deficiency and water-limitation is still debated. For well-watered conditions, the general consensus remains that stomatal functioning is well maintained even when leaf K concentrations are below the critical values for photosynthesis. Jákli et al. (2017) suggested that the reduction of stomatal conductance under K-deficient conditions is a reaction to low rates of CO₂ assimilation in order to maximize water-use efficiency.

In contrast to K, Mg has no active function in stomatal control. Therefore, the causality suggested by Sun et al. (2001) – who attributed decreased CO₂ assimilation in Mg-deficient Pinus radiata to reduced stomatal conductance – appears quite unlikely. The decline in net assimilation that is commonly observed under Mg deficiency is rather caused by non-stomatal factors. This assumption is supported by numerous studies reporting no effect of Mg deficiency on stomatal conductance or leaf-internal CO₂ concentrations (e.g. Lasa et al. 2000, Tang et al. 2012, Yang et al. 2012). However, unlike for K (Lu et al. 2016a, 2016b, Jákli et al. 2017), a quantitative analysis of photosynthetic limitations in Mg-deficient plants has not been published so far.

**Mesophyll conductance**

After entering the leaf through the stomatal pore, a series of resistances further object the movement of CO₂ through the leaf mesophyll and therefore affect the CO₂ concentration in chloroplasts. These resistances are aggregated as (their inverse) ‘mesophyll conductance’ to CO₂ diffusion and are summarized in a recent review by Berghuijs et al. (2016). After diffusion through the leaf internal air space, CO₂ dissolves in the apoplastic water of the cell walls. Once in the liquid phase, CO₂ is present as either dissolved CO₂ or HCO₃⁻ and further diffuses through the pores of the cell wall, the plasma membrane, the cytosol, the chloroplast envelope and the chloroplast stroma, where enzymatic CO₂ fixation is taking place.

There is common agreement that mesophyll conductance is reduced under low K supply, which is most commonly associated with leaf anatomical changes. Limitations to photosynthesis that originate from restricted CO₂ diffusion are attributable to mesophyll rather than stomatal conductance (e.g. Terry and Ulrich 1973, Jin et al. 2011, Battie-Laclau et al. 2014). Jákli et al. (2017) reported that the fraction of total photosynthesis limitation that results from mesophyll conductance increased from 45 to 64% in non-symptomatic leaf area of K-deficient sunflower compared to K-sufficient plants, and Lu et al. (2016a) showed an increase of mesophyll limitation from 28 to 50% in K-inefficient oilseed rape under low K supply. They did, however, not find a significant effect of K deficiency on mesophyll limitations in a K-efficient variety of oilseed rape. Battie-Laclau et al. (2014) could likewise not show an effect of K deficiency on mesophyll limitations in eucalyptus, although absolute values of mesophyll conductance declined, indicating species- and even variety-specific co-regulation between mesophyll- and biochemical limitations of photosynthesis.

Many variables affect the diffusion of CO₂ inside leaves. Gaseous diffusion is largely determined by leaf anatomical properties such as leaf thickness and the volume ratio of leaf-internal airspace to mesophyll cells,
which both affect the specific leaf mass (SLM). Numerous studies show that deficient K supply significantly increases SLM, (O’Toole et al. 1980, Cakmak et al. 1994b, Pettigrew 1999, Gerardaux et al. 2010, Jin et al. 2011, Lu et al. 2016b). SLM of K-deficient leaves are enhanced by decreased leaf thickness (O’Toole et al. 1980, Battie-Laclau et al. 2014) and reduced leaf-internal airspace (Zhao et al. 2001, Battie-Laclau et al. 2014). Moreover, K is an osmotic driver of cell extension and K deficiency results in smaller mesophyll cells (Mengel and Arneke 1982, Claussen et al. 1997). Decreased leaf thickness, leaf-internal airspace and cell size reduce the chloroplast surface area exposed to the leaf-internal airspace (Giuliani et al. 2013) and, thus, mesophyll conductance. In addition, Lu et al. (2016b) observed a greater distance between chloroplasts and cell walls in K deficient Brassica napus, increasing the overall pathway length for liquid phase CO₂ diffusion and, thus, mesophyll conductance.

Besides being affected by anatomical properties, an increase in SLM can also be attributed to an increase in non-structural carbohydrates within K-deficient leaves (Cakmak et al. 1994b, Gerardaux et al. 2010). Gerardaux et al. (2010) report that 15% of the SLM increase under K deficiency was attributed to an increase in soluble sugar concentrations. Based on purely physical studies by Carroll et al. (2014), Hölttä et al. (2017) suggested that an increase in sugar concentration could decrease the rate of liquid phase CO₂ diffusion. Increased concentrations of sugars in the liquid phase of the leaf mesophyll might therefore contribute to the reduction of mesophyll conductance under K deficiency.

Mesophyll conductance is not only sensitive to leaf anatomical traits and solute concentrations, but might additionally be affected by the expression of proteins such as aquaporins that facilitate leaf-internal CO₂ diffusion. Kanai et al. (2011) demonstrated the importance of adequate K nutrition for the functioning of aquaporins for water uptake and transport. There is strong evidence that the transport of not only water but also of CO₂ through plasma- and chloroplast-membranes is substantially supported by aquaporins, and it is reported that decreased expression of the tobacco aquaporin NaAQP1 can cause a 20% reduction in mesophyll conductance (Flexas et al. 2006, Uehlein et al. 2008). Although direct experimental evidence is still missing, an involvement of aquaporin activity in the overall decrease of mesophyll conductance under K deficiency is possible.

Furthermore, CO₂ diffusion through the cytosol and the chloroplast stroma is likely to be facilitated by the activity of carbonic anhydrases, a group of enzymes that catalyze the interconversion between CO₂ and HCO₃⁻ and might therefore increase the rate of CO₂ delivery to Rubisco (Berghuijs et al. 2017). Increased leaf K concentrations enhanced the activity of carbonic anhydrases in leaves of Brassica juncea (Mohammad and Naseem 2006), but a general evidence for the linkage between carbonic anhydrase activity and mesophyll conductance under K-deficient conditions is missing so far.

To summarize the effect of K deficiency on mesophyll conductance, we conclude that a decrease in photosynthesis under K deficiency can be largely attributed to an increase in leaf internal CO₂-transfer resistance, resulting in low mesophyll conductance. Increased sugar concentrations and SLM most likely contribute to the overall decline in mesophyll conductance. A reduction in chloroplast surface area exposed to the leaf-internal airspace and increased intracellular pathway length for liquid phase diffusion seem to be the most important factors limiting CO₂ mesophyll diffusion. The contribution of the different traits to the overall reduction of mesophyll conductance is highly species-specific (Tomás et al. 2013) and can also vary between varieties of the same species (Lu et al. 2016a, 2016b).

In contrast to K, no study exists on the relation between Mg nutrition and mesophyll conductance. We can hence only speculate on possible effects of Mg on the diffusion of CO₂ through the leaf mesophyll. Similar to K deficiency, increased SLM is reported for leaves of Mg-deficient plants (Cakmak et al. 1994b, Li et al. 2017), which is attributed to an accumulation of soluble carbohydrates as a consequence of impaired phloem loading (e.g. Cakmak et al. 1994b, Lavon et al. 1995). As discussed above, increased concentrations of sugars in the liquid phase of the leaf mesophyll might affect its conductivity to CO₂ diffusion. However, as mentioned previously, a systematic limitations analysis is needed to quantify the contribution of stomatal and mesophyll limitations to photosynthesis of Mg-deficient plants.

**Chloroplast ultrastructure**

The ultrastructure of chloroplasts is formed by the organization of the internal membrane system. Part of the membranes stack up into cylindrical structures, which form the so-called grana, while part of the membranes remains unstacked, the stroma lamellae. K⁺ and Mg²⁺ both facilitate a well-structured organization of grana and stroma lamellae, therefore support chloroplast integrity, the efficiency of light absorption, Rubisco diffusion and, as a consequence, carbon assimilation. Under Mg and K deficiency damage of chloroplast ultrastructure was observed as such that the lamella structure was irregular, loose and partly dispersed in the cytoplasm and the amount of grana and lamellae was reduced (Hall et al. 1972, Zhao et al. 2001, Jia et al. 2008). In contrast,
increasing Mg concentrations resulted in many distinguished stacked membranes (Rumak et al. 2010). Grana stacking mainly depend on van der Waals attraction forces and electrostatic repulsion (Puthiyaveetil et al. 2017). Electrostatic repulsion is controlled by membrane surface charges and the ion concentrations in the milieu surrounding the thylakoid membranes. Screening of net negative surface charges by K⁺ as a monovalent cation, and more efficiently Mg²⁺ as a divalent cation, reduces the electrostatic repulsion force. Puthiyaveetil et al. (2017) showed that at low K⁺ activities, stacking is hindered because repulsive forces dominate. In contrast, at high K⁺ and Mg²⁺ concentrations (>100 mM K⁺ and 5 mM Mg²⁺) grana stacking was well developed. Furthermore, it is suggested that changes in the lateral micro-organization of LHClIs and subsequent segregation of the two photosystems (PSs) occurs at low Mg²⁺ concentrations (Sys 1995, Stoitchkova et al. 2006). However, grana stacking require higher Mg²⁺ concentrations than the segregation of PSs (Stoitchkova et al. 2006).

Grana formation enhances the stromal volume, thus generates more space for free diffusion of macromolecules in the densely crowded stroma (Anderson et al. 2008). Enhancement of stromal volume might alleviate macromolecular crowding and thus, aid diffusion of Rubisco and facilitate high rates of carbon fixation (Anderson et al. 2008).

**Chlorophyll**

Chlorophyll a and b are the major pigments for the absorption of light energy and synthesis of both pigments requires Mg. A common response to Mg deficiency is the reduction of chlorophyll concentrations as demonstrated in numerous studies (Mengutay et al. 2013, Faust and Schubert 2016, Tränkner et al. 2016). However, considering chlorophyll a and b separately, the response is not uniform. In sugar beet, chlorophyll a and b concentrations decreased under Mg deficiency (Hermans et al. 2004). In coffee, the response is cultivar specific as there were no changes in the chlorophyll a/b ratio in cv. Catuai (Da Silva et al. 2014) whereas in cv. Acaiá chlorophyll a/b concentrations fluctuated over the experimental time without clear correlation with the Mg deficiency.

Biosynthesis of chlorophyll starts with the insertion of Mg into protoporphyrin IX (Fig. 1C). The insertion of Mg is catalyzed by Mg-chelatase, an enzyme consisting of 40, 70 and 140-kDa subunits, designated ChlI, ChlD and ChlH subunits, respectively. For the insertion of Mg into protoporphyrin IX, the catalytic cycle of Mg-chelatase undergoes two steps (Masuda 2008). The first step is the activation step where the subunits I and D form a complex with ATP and Mg²⁺. The subunit H binds to protoporphyrin IX and Mg²⁺, and presumably contains the active site for chelation. The second step includes the Mg chelation into protoporphyrin IX that requires ATP hydrolysis. In vitro studies demonstrated that chelation of 1 magnesium requires hydrolysis of 15 ATP, making Mg chelation an expensive reaction coupled to ATP hydrolysis (Reid and Hunter 2004). The activity of Mg chelatase is sensitive to free Mg concentrations and thus, depends on diurnal cycling. When illuminated, the free Mg concentrations in the chloroplast stroma can increase up to 6 mM allowing a flux into the chlorophyll biosynthetic pathway (Reid and Hunter 2004). Vicia faba plants grown under Mg-deficient conditions showed a decrease in the transcript abundance of Mg chelatase subunit H even in tissues where the Mg concentrations did not fall below the critical level (Neuhaus et al. 2013). Hence, analysis of Mg chelatase H transcript abundance might function as an early indicator for Mg deficiency.

The biosynthesis of chlorophyll primarily generates chlorophyll a. Part of the chlorophyll a is oxidized to chlorophyll b by chlorophyllide a oxygenase, but chlorophyll b can be reduced back to chlorophyll a. For chlorophyll degradation, chlorophyll b must be first converted to chlorophyll a as chlorophyll b derivatives are not catalyzed in the subsequent pathway. Thus, the ratio of both pigments is tightly regulated by the interconversion of chlorophyll a and b (chlorophyll cycle) (Blankenship 2014, Sato et al. 2014). Chlorophyll a and b are related to the stability of the light harvesting complex II (LHCII) and chlorophyll b is crucial for LHCII accumulation (Sato et al. 2015). Degradation of chlorophyll b triggers degradation of LHCII and thus participates in the regulation of the plant light-harvesting capacity and the suppression of photodamage. It also promotes nutrient remobilization as LHCII is a highly abundant protein in the chloroplast and serves as a reservoir of nutrients under deficiency (Sato et al. 2015). Thus, chlorophyll degradation under Mg deficiency can function to release Mg and to protect cells from photodamage by triggering LHCII degradation.

Similarly, the total concentration of chlorophyll has been frequently reported to decrease under K deficiency (Longstreth and Nobel 1980, Bednarz and Oosterhuis 1999, Zhao et al. 2001, Lu et al. 2016b). It has been suggested, however, that chlorophyll degeneration is not a primary effect of K deficiency, but is rather attributed to an excessive production of ROS (Cakmak 2005) that will be referred to later in the text.

**Rubisco activation and activity**

Magnesium is crucial for CO₂ fixation as it is directly involved in the activation and activity of Rubisco.
Furthermore, Mg is crucial for protein synthesis, which affects Rubisco protein abundance and thereby, indirectly influences CO₂ fixation. Under Mg deficiency, protein concentrations were shown to be reduced in sugar beet (Faust and Schubert 2016), wheat (Mengutay et al. 2013) and maize (Mengutay et al. 2013). Lower protein concentrations under Mg deficiency might be due to the involvement of Mg ions in ribosomal subunit association and activity (Yamamoto et al. 2010). Furthermore, Mg is suggested to control the structural flexibility of numerous ribosomal proteins (Yamamoto et al. 2010). More than 100 magnesium ions are associated with the large ribosomal subunit (Petrov et al. 2012) and part of the Mg ions form magnesium microcluster, which contain two tightly associated Mg ions. Magnesium microclusters are suggested to provide structural integrity to the large ribosomal subunit and assist in maintaining the compact native structure of the assembly (Petrov et al. 2012). The most abundant protein on earth is Rubisco, and about 30% of the total protein in a plant leaf (Jensen 2000) and approximately 40% of all stromal proteins is Rubisco (Hazra et al. 2015). By proteomic analysis, Peng et al. (2015) showed that the protein abundance of Rubisco and Rubisco activase (Rca) was decreased under Mg deficiency in Citrus sinensis, indicating that Rubisco quantity and activity are affected which agreed with an 88% reduction of assimilation rates in Mg-deficient leaves. However, the CO₂ fixation is rather controlled by the amount of active Rubisco, than by the total amount of Rubisco protein (Taylor and Andersson 1996).

Rubisco activity is commonly measured in in vitro assays, whereas in vivo determination of CO₂ assimilation rates can serve as a measure for Rubisco activity. Numerous studies show decreased Rubisco activity or CO₂ assimilation rates under Mg deficiency in various plant species such as spinach (Yuguan et al. 2009), citrus (Tang et al. 2012, Li et al. 2017), maize (Jezek et al. 2015), sunflower (Lasa et al. 2000) and P. radiata (Laing et al. 2000, Sun et al. 2001). The Rubisco activity is sensitive to the Mg status as observed by a decline in CO₂ assimilation rates in Mg-deficient sugar beet and barley already 7 and 8 days, respectively, after onset of Mg deficiency in nutrient solution trials (Terry and Ulrich 1974, Tränkner et al. 2016). Rubisco catalyzes the carboxylation and/or the oxygenation of ribulose-1,5-bisphosphate (RuBP) and thereby initiates the sugar producing or photorespiratory pathway. To exhibit catalytic activity, a lysine residue in the active site of the enzyme has to be carbamylated by an activator, non-substrate CO₂ molecule and the labile carbamate group is subsequently stabilized by an Mg ion prior to binding of the substrate RuBP (Taylor and Andersson 1997, Portis 2003). However, the loss of the activator CO₂ and Mg ion can lead to tight binding of the substrate RuBP or other sugar phosphates without prior carbamylation, inhibiting its activity (Taylor and Andersson 1997). Kim and Portis (2006) show that low Mg concentrations increased dramatically the rate of deactivation of Rubisco and relate this to decarbamylation of active sites and stronger binding of RuBP to the uncarbamylated form of Rubisco. The release of the bound RuBP and other sugar phosphates is achieved by the catalytic chaperone Rca (Kuriata et al. 2014). Rca has a hydrolytic ATPase activity, which is required for the Rubisco activating activity. When Mg was absent from the assay medium, enzymatic turnover was abolished in isolated tobacco Rca (Hazra et al. 2015). Similarly, the Rca activity was decreased in Mg deficient spinach (Yuguan et al. 2009). Hazra et al. (2015) suggest that a second protein-based magnesium-binding site exists which serves as a co-activator by mediating contact between the subunits. Thus, both Mg coordinated with ATP and Mg for promoting subunit assembly is required and the fully activated complex is best represented by Rca•Mg•ATP•Mg (Hazra et al. 2015). The catalytic activation of Rca is Mg specific, as a replacement of Mg²⁺ by Mn²⁺ resulted in a 32-fold decrease in turnover rates.

High-cytosolic sucrose concentrations in Mg deficient leaves, which is a common phenomenon under Mg deficiency, resulting from reduced rates of phloem export (Cakmak et al. 1994a), are also supposed to repress the expression of genes involved in photosynthesis (Neales and Incoll 1968, Jang and Sheen 1994, Sheen 1994).

Likewise, K deficiency reduces Rubisco carboxylation activity in chloroplasts. This was shown by in-vitro measurements (Weng et al. 2007, Hu et al. 2015, Zahoor et al. 2017) as well as by estimations of the maximum Rubisco carboxylation velocity, V₅₀, from combined measurements of leaf gas exchange and chlorophyll fluorescence (Jin et al. 2011, Battie-Laclau et al. 2014, Erel et al. 2015, Jákli et al. 2017). It is sometimes stated that K deficiency inhibits the activation of Rubisco (Oosterhuis et al. 2013), resulting in reduced rates of RuBP carboxylation. In an early report on the subject, Peoples and Koch (1979) clearly state that, in a purified Rubisco extract of K-deficient and K-sufficient alfalfa, the specific activity of RuBPc (=RuBP-carboxylase) isolated from severely K-deficient and K-sufficient leaflets was not significantly different, suggesting that K does not function in RuBPc activity’. In contrast, when measuring carboxylation activity in a crude extract, the authors found significantly increased activity of Rubisco extracted from K sufficient leaves. They came to the conclusion that the biosynthesis of Rubisco was markedly suppressed under deficient K supply. This was again shown in cucumber.
cotedledons (Ohya et al. 1986). Generally, protein synthesis appears to be sensitive not only to Mg but also to K deficiency, because K+ is involved in ribosomal translation (Nissen 2000, Austin and First 2002). Hence, the concentration of soluble proteins in plant tissues is reduced under K deficiency, whereas the concentration of free amino acids increases (Besford 1975, Cakmak et al. 1994a, Li et al. 1997, Faust and Schubert 2016). As a consequence, the quantity of Rubisco is reduced in K-deficient leaves. Lower Rubisco content (on a leaf area basis) was also shown in K-deficient soybean leaves (Wang et al. 2015), but neither total soluble protein nor Rubisco content was affected by K status in citrus leaves (Lavon et al. 1999). The authors, however, report higher total amino acid content and Rubisco carboxylation activity. Nonetheless, the effect of K on quantitative Rubisco characteristics appears to be dependent on the species under study and the respective growth stage (Osaki et al. 1993).

Apart from Rubisco quantity, K supply can indirectly affect Rubisco activity. Optimum chloroplastic K+ concentrations (i.e. in the range of cytosolic K+ concentrations around 100 mM) induce a broader range of pH optimum for Rubisco functioning than under K deficiency (Mengel and Kirkby 2001). Furthermore, downregulation of Rubisco activity may occur under low chloroplastic CO2 concentrations (Galmés et al. 2011), which is a result of reduced CO2 transfer rates in K-deficient mesophyll tissues (Jákli et al. 2017). Comparable to Mg deficiency, reduced rates of phloem export result in high-cytosolic sucrose concentrations (Cakmak et al. 1994a) that can cause feedback inhibition of Rubisco activity (Goldschmidt and Huber 1992).

Additionally, Jin et al. (2011), Battie-Laclau et al. (2014) and Erel et al. (2015) report reduced maximum electron transport rates (jmax) through PS of K-deficient hickory, eucalyptus and olive leaves, respectively. jmax is associated with the ATP- and NADP+ consuming RuBP regeneration (Farquhar et al. 1980), implying less acceptor molecules for CO2 fixation.

To summarize, there is no evidence that K+ is involved in Rubisco activation, but rather regulates Rubisco activity by affecting its quantity, its pH-optimum and substrate (CO2 and possibly RuBP) availability.

**K and Mg involvement in photoassimilate translocation**

Plant growth and metabolism require the translocation of carbohydrates from photosynthetically active tissues into sink organs such as roots, flowers and seeds. Loading of sucrose – the major transport form of carbohydrates in plants – into the phloem is substantially affected by K and Mg nutrition (Fig. 1E) and a shortage of either of these elements may substantially affect the efficiency of the long-distance carbon transport within plants. According to the pressure flow hypothesis initially developed by Münch (1930), the movement of solutes in the phloem follows a hydrostatic pressure gradient that originates from differences in solute concentrations. K+ is the most abundant cation in the phloem and, together with sucrose and amino-N compounds, is the most important osmotic compound of the phloem sap. It therefore contributes to the rate of phloem transport (Lalonde et al. 2003), and K+ concentration within the phloem sap of *Ricinus communis* was positively correlated with the level of external K supply (Mengel and Haeder 1977).

In apoplastic phloem loading, sucrose has to be actively transported against its concentration gradient across the plasma membranes of phloem companion cells and sieve elements by sucrose transporters. The necessary energy is generated by H+·ATPases, which create a proton gradient across the plasma membrane (Michelet and Boutry 1995). Low cellular Mg concentrations can result in dissociation of the Mg·ATP complex and in a decreased activity of plasma membrane H+·ATPases (Hanstein et al. 2011). As a consequence, the transmembrane proton gradient cannot be established, the rate of phloem export declines and sucrose accumulates in the leaf tissue.

Besides Mg, K is crucially involved in sucrose loading. A study on Arabidopsis *akt2/3-1* knockout mutants revealed that the transmembrane potential established by H+·ATPases is regulated by the inward-rectifying AKT2/3 potassium channel (Deeken et al. 2002). AKT2/3 therefore contributes to the basic loading and unloading of sucrose into and from the phloem. By multiple post-translational modification steps it can be converted to a non-rectifying channel, which facilitates a rapid efflux of K+ from the sieve element/companion cells complex (Gajdanowicz et al. 2011, Sandmann et al. 2011). The established K+ gradient provides energy that is used by other transporters for phloem loading. This mechanism, the so-called ‘potassium battery’, serves as a mobile energy source to overcame local ATP-shortages and maintain the efficiency of the long-distance transport system (Gajdanowicz et al. 2011, Dreyer et al. 2017).

An impaired source-to-sink carbon allocation under Mg deficiency was shown in numerous plants such as sugar beet (Hermans et al. 2005), maize (Mengutay et al. 2013), bean (Cakmak et al. 1994a) and soybean (Yang et al. 2017). Besides sucrose, starch can accumulate in the chloroplast under Mg deficiency (Lavon et al. 1995, Ceylan et al. 2016, Yang et al. 2017). The molecular regulation underlying carbon accumulation under Mg...
deficiency is still ambiguous. In sugar beet, the transcript abundance of the specific H^+/sucrose symporter BvSUT1 was higher in Mg-deficient leaves, but sucrose contents were increased (Hermans et al. 2005). In V. faba, the transcript abundance of plasma membrane H^+-ATPase isoforms was decreased when plants were grown under Mg-deficient conditions (Neuhaus et al. 2013). However, this was not the case for all examined isoforms. One isoform showed slightly increased transcript abundance under Mg deficiency and another isoform could only be found in the Mg-deficient treatment and was absent under control Mg supply (Neuhaus et al. 2013).

Similar to Mg, a shift in the partitioning of assimilates— with increased concentrations of carbohydrates in primary leaves and reduced concentrations in roots—as well as reduced rate of phloem export of sucrose were observed in K-deficient Phaseolus vulgaris (Cakmak et al. 1994a, 1994b). Likewise, sucrose concentration was increased in functional leaves of K-deficient cotton (Bednarz and Oosterhuis 1999, Hu et al. 2015, Zahoor et al. 2017).

These studies clearly show the strong influence of Mg and K on carbon assimilation and allocation. However, it remains ambiguous how Mg and K status, carbohydrate accumulation and carbohydrate-triggered feedback on photosynthesis in physiological and molecular aspects are linked.

### K and Mg involvement in photoprotection

As outlined in the previous paragraphs, K and Mg affect the photosynthetic capacity and a deficiency of either one of the two nutrients decreases CO_2 assimilation (Fig. 2). Under this limitation of photosynthetic capacity, the absorbed light energy is in excess to what can be used in photosynthesis processes, leading to an enhanced production of ROS and plants suffer oxidative stress (Nishiyama et al. 2006, Takahashi and Badger 2011). ROS inhibit the repair of photodamaged PSII, predominantly the D1 protein in the reaction center of PSII, causing photoinhibition (Takahashi and Badger 2011, Järvi et al. 2013). Photoinhibition can be indicated by the chlorophyll fluorescence parameter F_v/F_m (Niyogi 1999), which describes the maximum efficiency at which light absorbed by PSII is used for the reduction of Q_A, the primary quinone electron acceptor in PSII (Baker 2008). Mg- and K-deficiency induce non-uniform responses in F_v/F_m. In Mg-deficient Citrus and sugar beet, F_v/F_m was decreased (Hermans et al. 2004, Tang et al. 2012, Yang et al. 2012) whereas in Mg-deficient sunflower and Sulla carnosa, F_v/F_m was unaffected (Lasa et al. 2000, Farhat et al. 2015). Changes in F_v/F_m under Mg-deficiency were related to damage of the oxygen-evolving complex on PSII or to an accumulation of reduced Q_A (Yang et al. 2012). K deficiency induced a decrease of F_v/F_m in two cotton cultivars (Wang et al. 2012), in rice (Jia et al. 2008), olive (Erel et al. 2015) and in maize (Qu et al. 2013), whereas in Norway spruce and sunflower a decrease in F_v/F_m was not observed (Barnes et al. 1995, Jäklí et al. 2017). Two soybean cultivars being tolerant and sensitive to K deficiency, respectively, responded differently to K deficiency: the tolerant cultivar did not show altered F_v/F_m values, whereas the sensitive cultivar showed a significant decrease of F_v/F_m (Wang et al. 2015). In conclusion, Mg- and K-deficiency do not commonly induce photoinhibition, which might depend on the magnitude of deficiency of Mg and K in the leaf tissue, cultivar specific responses and environmental and experimental conditions.

### ROS scavenging

The ROS species that are produced in the thylakoid have to be immediately detoxified before they diffuse from their generation site and damage targeted molecules (Asada 2006). Detoxification in the chloroplast is achieved by antioxidants such as ascorbate peroxidase (APX), Fe- and CuZn-superoxide dismutase (SOD) and glutathione reductase (GR). The interplay between ROS formation and ROS detoxification is strictly controlled and necessary for unrestricted photochemistry. Mg- and K-deficiency induce commonly elevated ROS levels and enhanced ROS-detoxifying enzyme activity. Under low K and Mg supply, increased H_2O_2 or O_2^- concentrations have been reported on numerous plants species such as Arabidopsis, maize, rice, cotton and coffee (Shin and Schachtman 2004, Weng et al. 2007, Hu et al. 2016, Da Silva et al. 2017). A K-inefficient cotton cultivar increased O_2^- and H_2O_2 leaf concentrations, and increased activities of SOD and APX, whereas a K-efficient cotton cultivar only increased APX, but not SOD activity, and neither H_2O_2 nor O_2^- concentrations were affected (Wang et al. 2012). Özgür Uzılday et al. (2017) showed the clear impact of the Mg status on ROS generation. When Mg was absent from the nutrient solution or supplied only with 75 μM, the H_2O_2 concentration in cotton leaves was increased by 29 and 33%, respectively, but when the Mg supply was raised to 150 μM, the H_2O_2 concentration was increased by 13%. Similarly, barley leaves suffering severe Mg deficiency had up to 55% higher H_2O_2 concentration compared to control, though the activity of APX, GR and SOD were substantially increased. Under mild deficiency, the activity of APX, GR and SOD were still increased, but the concentration of H_2O_2 was decreased to the same level as the control, indicating that under severe Mg
deficiency the extent of H$_2$O$_2$ production exceeded the scavenging capacity (Tränkner et al. 2016).

In conclusion, K and Mg deficiencies induce oxidative stress indicated by increased H$_2$O$_2$ and O$_2$•$^-$ levels, but in response the antioxidant enzyme activity is enhanced, which detoxifies part of the ROS. However, ROS cannot always be decreased to levels comparable to levels in unstressed plants, depending on the stress level induced by K- and Mg-deficiency.

**Non-photochemical quenching**

The non-photochemical dissipation of excess absorbed light energy as heat, commonly determined as NPQ which is located in LHCII antenna, is an important photoprotective mechanism (Ruban 2016). Thermal energy dissipation as a photoprotective mechanism can dissipate up to 75% of absorbed light energy (Niyogi 1999). Plants increase the dissipation of energy as heat in response to Mg and K deficiency in order to protect...
the absorption of CO$_2$ from intercellular airspaces (Takahashi and Badger 2011). In B. napus leaves, chloroplasts responded to K deficiency by increasing their distance from the cell wall (Lu et al. 2016b). Usually, chloroplasts are allocated at the cell surface to absorb CO$_2$ and light. However, the study of Lu et al. (2016b) focuses on CO$_2$ diffusion conductance in the mesophyll and does not consider light absorption. Nevertheless, it revealed altered chloroplast organization under K deficiency, but further studies are needed to describe this effect with regard to photoprotection. The same applies for Mg, where studies of chloroplastic movement in response to Mg deficiency are completely absent from the present literature.

**Leaf movement**

Paraheliotropic leaf movement is a mechanism by which absorption of excess light and a resulting excessive excitation pressure to the reaction centers is avoided. In Robinia pseudoacacia, paraheliotropic leaf movement resulted in an effective mean to alleviate high-light stress on PSII (Arena et al. 2008). The level of F$_v$/F$_m$ measured in the late afternoon was comparable to those in the morning, whereas in leaves in which the rachis was fixed to prevent leaf and leaflet movement, F$_v$/F$_m$ was reduced in the late afternoon. The authors suggest that the absence of recovery indicate a PSII damage assuming that F$_v$/F$_m$ is a good indicator for photoinhibition (Arena et al. 2008). Similarly, in young soybean leaves, changes in the petiole and midrib angle reduced the light intensity on the leaf surface and helped to protect leaves against high irradiance (Jiang et al. 2006). Paraheliotropism was shown to be a protection strategy against photoinhibition in water-stressed bean cultivars (Pastenes et al. 2004) and Vitis californica (Gamon and Pearcy 1989). We observed strong heliotropic leaf movements in sunflower grown under K deficiency (unpublished data). We suggest that beside the above-mentioned effects of leaf movement on microclimate, paraheliotropism might play a role in protecting sunflower leaves from excessive light. An indication is that leaf areas showing K deficiency symptoms, are almost shaded from any light incidence. However, in sunflower this phenomenon seems to be K-specific as Mg-deficient plants did not show such behavior. To our knowledge, no study on paraheliotropism under K deficiency and its contribution to photoprotection exists. Further research should be conducted to reveal whether paraheliotropic leaf movement is an active strategy of photoprotection or whether it is a reaction to reduced turgor under K deficiency. In case it is an active strategy under low-cellular K$^+$ status, leaf movement might be a preferred strategy as it is a turgor-driven and thus
a K requiring process (Oosterhuis et al. 2014), hence K+ ions preferentially need to be allocated to the sites where leaf angle is controlled.

**Summary**

Mg and K are directly and indirectly involved in numerous physiological processes associated to photosynthesis (Fig. 2). A decline in the rate of net carbon assimilation is observed when either of the nutrients cannot be absorbed by plants in sufficient quantity, and its leaf tissue concentration drops under a critical value. Primary effects of K deficiency, that can be associated with a reduction of the photosynthetic capacity or CO₂ assimilation, are (1) decreased protein synthesis, and therefore Rubisco quantity, (2) anatomical alterations in leaf structure reducing mesophyll conductance and thus chloroplastic CO₂ concentration and (3) chloroplast ultrastructure. Although K is involved in the osmoregulation of stomatal guard cells, K deficiency does not impede stomatal functioning and the optimization of photosynthetic water-use efficiency. Primary effects of Mg deficiency also include protein and Rubisco synthesis as well as chloroplast ultrastructure. In contrast to K, Mg directly functions in chlorophyll synthesis and Rubisco activation, but no effect of Mg deficiency on leaf anatomy or mesophyll conductance is reported. Both K and Mg directly affect the phloem loading of sucrose, and a deficiency in those nutrients results in an accumulation of sucrose in source tissues, causing further down-regulation of Rubisco activity. Photoprotective mechanisms respond to both K and Mg deficiency, with the potential of decreased Fv/Fm and enhanced NPQ, antioxidant enzyme activity and photorespiration. The manifold effects of plant anatomy, physiology and biochemistry on photosynthesis, photosynthetic translocation and photoprotection under conditions of K and Mg deficiency are characterized by complex interactions and inter-regulatory mechanisms, and many questions still remain to be answered.

**Author contributions**

M.T. and B.J. conceived, proofread and formatted the manuscript in equal contributions. M.T. wrote the sections related to Mg deficiency. E.T. wrote the sections related to ROS and antioxidants. B.J. wrote the sections related to K deficiency.

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**References**


Carroll MJ, Slaughter LH, Krouse JM (1994) Turgor potential and osmotic constituents of Kentucky Bluegrass leaves supplied with four levels of potassium. *Agron J* 86: 1079


Ceylan Y, Kutman UB, Mengutay M, Cakmak I (2016) Magnesium applications to growth medium and foliage affect the starch distribution, increase the grain size and improve the seed germination in wheat. *Plant and Soil* 406: 145–156


Faurholdt RB, Schnepf S (2016) Protein synthesis is the most sensitive process when potassium is substituted by sodium in the nutrition of sugar beet (*Beta vulgaris*). *Plant Physiol Biochem* 107: 237–247


Goldschmidt EE, Huber SC (1992) Regulation of
boths alters sugar partitioning and phloem loading in young mature leaves. Planta 220: 541–549
affects carbohydrate metabolism in the leaf subtending the cotton (Gossypium hirsutum L.) boll and its
relationship with boll biomass. F Crop Res 179: 120–131
deficiency on antioxidant metabolism related to leaf
senescence in cotton (Gossypium hirsutum L.). F Crop Res 191: 139–149
Humble GD, Raschke K (1971) Stomatal opening
quantitatively related to potassium transport evidence
deficient sunflower and their implications on water-use
Plant Cell 6: 1665–1679
of the thylakoid lumen in photosynthesis regulation.
Front Plant Sci 4: 434
Jensen RG (2000) Activation of Rubisco regulates
photosynthesis at high temperature and CO2. Proc Natl
Acad Sci USA 97: 12937–12938
Photosynthetic capacity, nutrient status, and growth of
maize (Zea mays L.) upon MgSO4 leaf-application. Front
Plant Sci 5: 1–10
deficiency on chloroplast ultrastructure and chlorophyll
fluorescence in inefficient and efficient genotypes of rice. J Plant Nutr 31: 120–131
orientation, photorespiration and xanthophyll cycle
protect young soybean leaves against high irradiance in
GH, Chen M (2011) Effects of potassium supply on
limitations of photosynthesis by mesophyll diffusion
conductance in Carya cathayensis. Tree Physiol 31:
1142–1151
Kanai S, Moghaieb RE, El-Shemy HA, Panigrahi R,
Mohapatra PK, Ito J, Nguyen NT, Saneoka H, Fujita K

gradients serve as a mobile energy source in plant
Rubisco activity in Mediterranean species is regulated by
the chloroplastic CO2 concentration under water
Gamon JA, Peary RW (1989) Leaf movement, stress
avoidance and photosynthesis in Vitis californica.
Oecologia 79: 475–481
Gerardeaux E, Jordan-Meille L, Constantin J, Pelerin S,
Dingkuhn M (2010) Changes in plant morphology and
dry matter partitioning caused by potassium deficiency
in Gossypium hirsutum [L.]. Environ Exp Bot 67:
451–459
plants – involvement in K+ acquisition, redistribution
and homeostasis. FEBS Lett 581: 2348–2356
Giuliani R, Koteveya N, Voznesenskaya E, Evans MA,
Cousins AB, Edwards GE (2013) Coordination of leaf
photosynthesis, transpiration, and structural traits in rice
and wild relatives (Genus Oryza). Plant Physiol 162:
1632–1651
Goldschmidt EE, Huber SC (1992) Regulation of
photosynthesis by end-product accumulation in leaves
of plants storing starch, sucrose, and hexose sugars.
Plant Physiol 99: 1443–1448
Gransee A, Fühs H (2013) Magnesium mobility in soils as
a challenge for soil and plant analysis, magnesium
fertilization and root uptake under adverse growth
conditions. Plant and Soil 368: 5–21
Haberl H, Erb KH, Krausmann F, Gauve V, Bondeau A,
appropriation of net primary production in earth’s
terrestrial ecosystems. Proc Natl Acad Sci USA 104:
12942–12947
Hall JD, Barr R, Al-Abbas AH, Crane FL (1972) The
ultrastructure of chloroplasts in mineral-deficient maize
Hanstein S, Wang X, Qian X, Friedhoff P, Fatima A, Feng K,
Schubert S (2011) Changes in cytosolic Mg2+
levels can regulate the activity of the plasma membrane H+-ATPase
in maize. Biochim J 435: 93–101
Hazra S, Henderson JN, Liles K, Hilton MT, Wachter RM
(2015) Regulation of ribulose-1,5-biphosphate
carboxylase/oxygenase (Rubisco) activase: product
inhibition, cooperativity, and magnesium activation.
J Biol Chem 290: 24222–24236
Heenan DP, Campbell LC (1981) Influence of potassium
and manganese on growth and uptake of magnesium
by soybeans (Glycine max (L.) Merr. cv. Bragg).
Plant and Soil 61: 447–456
Physiological characterisation of magnesium deficiency
in sugar beet: acclimation to low magnesium
differentially affects photosystems I and II. Planta 220:
344–355
Hermans C, Bourgis F, Faucher M, Strasser RJ, Delrot S,
Verbruggen N (2005) Magnesium deficiency in sugar
beets alters sugar partitioning and phloem loading in young mature leaves. Planta 220: 541–549

Physiol. Plant. 163, 2018

427
Potassium deficiency affects water status and photosynthetic rate of the vegetative sink in green house tomato prior to its effects on source activity. Plant Sci 180: 368–374


Masuda T (2008) Recent overview of the Mg branch of the tetrapyrrole biosynthesis leading to chlorophylls. Photosynth Res 96: 121–143

Mengel K, Arneke W-W (1982) Effect of potassium on the water potential, the pressure potential, the osmotic potential and cell elongation in leaves of Phaseolus vulgaris. Physiol Plant 54: 402–408


Münch E (1930) Die Stoffbewegungen in der Pflanze. Gustav Fischer, Jena, Germany


Özgür Uzılday R, Uzılday B, Yalçinkaya T, Türken I (2017) Mg deficiency changes the isoenzyme pattern of reactive oxygen species-related enzymes and regulates NADPH-oxidase-mediated ROS signaling in cotton. Turkish J Biol 41: 868–880


