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REVIEW

Effects of magnesium deficiency on photosynthesis and carbohydrate partitioning

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Abstract Magnesium nutrition is often forgotten, while its absence adversely affects numerous functions in plants. Magnesium deficiency is a growing concern for crop production frequently observed in lateritic and leached acid soils. Competition with other cations (Ca^{2+}, Na^{+}, and K^{+}) is also found to be an essential factor, inducing magnesium deficiency in plants. This nutrient is required for chlorophyll formation and plays a key role in photosynthetic activity. Moreover, it is involved in carbohydrate transport from source-to-sink organs. Hence, sugar accumulation in leaves that results from the impairment of their transport in phloem is considered as an early response to Mg deficiency. The most visible effect is often recorded in root growth, resulting in a significant reduction of root/shoot ratio. Carbohydrate accumulation in source leaves is attributed to the unique chemical proprieties of magnesium. As magnesium is a nutrient with high mobility in plants, it is preferentially transported to source leaves to prevent severe declines in photosynthetic activity. In addition, Mg is involved in the source-to-sink transport of carbohydrates. Hence, an inverse relationship between Mg shortage and sugar accumulation in leaves is often observed. We hereby review all these aspects with a special emphasis on the role of Mg in photosynthesis and the structural and functional effects of its deficiency on the photosynthetic apparatus.

Keywords Magnesium deficiency · Cation competition · Photosynthesis · Carbohydrate partitioning

Introduction

Magnesium (Mg) is a macronutrient often forgotten in crop production (Cakmak and Yazici 2010). In the last decades, several studies examined the relationship between Mg nutrition and plant growth in a number of higher plants (Fischer and Bremer 1993; Cakmak et al. 1994a; Fischer et al. 1998; Hermans et al. 2004, 2005; Hermans and Verbruggen 2005). Authors were more interested in its deficiency than in its toxicity, which was explained by a difficulty to detect toxicity symptoms even with high concentrations (Shaul et al. 1999). Hawkesford et al. (2012) attributed this shortage in toxicity reports to a great capacity of the vacuole to store magnesium within plant cells.

Despite the well-known number of functions attributed to magnesium, its deficiency in soils is a growing concern for high-productivity agriculture (Cakmak and Yazici 2010). This problem is common in soils fertilized only with N, P, and K, which may prevent Mg uptake. Similar antagonistic effect was also noticed in the presence of other competing cations, such as Ca^{2+}, H^{+}, NH_4^{+}, and Al^{3+}. Magnesium deficiency was found as well to be a critical concern in lateritic and leached sandy acid soils due to its potential for leaching (Mengel and Kirkby 2001; Shaul 2002; Cakmak and Yazici 2010; Gransee and Führs 2013). Its symptoms appear as leaf interveinal chlorosis with a development of chlorotic and necrotic lesions in

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later stages (Marschner and Cakmak 1989; Cakmak and Marschner 1992; Cakmak and Kirkby 2008). The main targets of Mg deficiency are photosynthesis and sugar transport from source-to-sink organs. In this work, we review Mg nutrition and deficiency in plants with a special emphasis on photosynthesis and carbohydrate partitioning.

Magnesium in the soil

Sprengel (1828) affirmed that "…when a plant needs 12 substances to develop, it will not grow if any one of these is not available in a sufficiently large amount as required by the nature of plants". According to Maguire and Cowan (2002), Mg is the eighth most abundant mineral element on earth. The source rock material from which it originates is that containing different types of silicates, and magnesium contents depend on silicate types (muscovite > biotite > hornblende > augite > olivine). As compared to other cations (Ca^{2+}, K^+, and NH_4^+), Mg^{2+} is relatively mobile in soils. The importance of magnesium derives from its chemical properties (size, charge, density, and structure) that make it unique amongst biological cations (Kehres and Maguire 2002). It is characterized by a high hydrated radius and sorbs weakly to soil colloids. It is therefore prone to leaching, mainly in acidic soil with low cation exchange capacity (Aitken et al. 1999; Grzebisz 2011), being the most important factor in decreasing Mg^{2+} availability for roots (Hermans et al. 2004). The effects of cation competition (Ca^{2+}, K^+, and Na^+) were also found to significantly reduce Mg^{2+} availability (Broadley and White 2010). This scarcity can be accentuated with N, P, and K fertilizers without simultaneous Mg fertilization (Verbruggen and Hermans 2013). In summary, two reasons can explain magnesium deficiency: absolute deficiency and cation competition. Absolute deficiency is due to: (1) Mg contents in source rocks (Papenfuß and Schlichting 1979) and (2) Mg mobilization and leaching (Schachtschabel 1954; Grzebisz 2011). Cation competition can be natural or induced by the abusive use of fertilizers (Cakmak and Yazici 2010); it strongly inhibits Mg uptake by nutrient imbalances (Gransee and Führs 2013). Abiotic stress conditions, such as drought and heat, can severely aggravate Mg deficiency by the inhibition of its uptake, since it is transported by mass flow (Gransee and Führs 2013). By contrast, Cakmak and Yazici (2010) stated specific benefits of Mg in the protection of soils from Al toxicity. Indeed, it was reported that magnesium can play an important role in alleviating Al toxicity in acid soils with only micromolar levels in comparison with Ca that is needed in millimolar concentrations (Silva et al. 2001).

Magnesium roles in plants

Magnesium is an essential macronutrient for the plant growth and development (Gransee and Führs 2013) and numerous key functions in plants (Cakmak and Yazici 2010). Its strong electrophilic axial coordination due to its tendency to form octahedral complexes enables it to occupy the central position in chlorophyll molecule (Beale 1999). Mg is also a phloem-mobile nutrient and its remobilization occurs from older leaves to younger ones (Taiz and Zeiger 2010). According to Cakmak and Yazici (2010), up to 35 % of the total Mg content in plants is located in chloroplasts, and the fraction remove of Mg pool directly associated with chlorophyll molecules constitutes 15–20 % of the total leaf content (Mengel and Kirkby 1987; Wilkinson et al. 1990). The remaining fraction (80–85 %) is present in mobile forms (Marschner 2012), which may explain the importance of Mg in photosynthate export. According to Cakmak and Yazici (2010), the importance of magnesium in phloem loading is related to its interaction with ATP fuelling; the H^+-ATPase enzyme which provides energy for phloem loading process and maintains sucrose transport into phloem cells.

Mg is considered as a cofactor and allosteric modulator for more than 300 enzymes, including carboxylases, phosphatases, kinases, RNA polymerases, and ATPases. It also plays in important role in chelation with nucleotide tri- and di-phosphate forms (Pakrasi et al. 2001; Cowan 2002; Shaul 2002; Hawkesford et al. 2012), in addition to its involvement in the electron transport chain in chloroplasts (Ding et al. 2006). It is also known that magnesium has an essential role in cell energy balance due to its interaction with various metabolites, mainly nucleoside tri- and diphosphates (Igamberdiev and Kleczkowski 2003). Cakmak and Yazici (2010) reported that Mg is involved in some other functions, such as protein synthesis and reactive oxygen species (ROS) generation. The importance of Mg in grana stacking was reported by Kaftan et al. (2002), and LHCII was found to participate in that cation-mediated formation of grana apart of being the major antenna for PSII (Hermans et al. 2004).

Mg stresses in plants

Mg concentrations in soil solutions are generally considered between 125 µM and 8.5 mM (Niu et al. 2014). Their variation is related to different factors: texture and cation exchange capacity of the soil (Hariadi and Shabala 2004), water availability, competing cation concentration, crop cultivation, and fertilizer regime (Broadley et al. 2008; Mikkelsen 2010). Hence, below 125-µM Mg plants may be subjected to Mg deficiency, while above 8.5 mM, they may face toxic effects that impair their growth and development (Guo et al. 2015). According to Tisdale et al. (1993), magnesium concentration in soil solution is typically between 0.2 and 2 mM in many soils of temperate regions. However, under some environmental conditions, many species (pasture, maize, potato, sugar beet…) can suffer from Mg deficiency even at these levels of available magnesium (Tan et al.1991; Tisdale et al. 1993; Hailes et al. 1997; Aitken et al. 1999).

Mg toxicity

Mg toxicity is a common problem in serpentine soils formed by the weathering of ultramafic rocks, such as in California (Brady et al. 2005) and Serbia areas (Vicić et al. 2014). These soils are known by macronutrient deficiencies (Ca, N, P, K), macronutrient toxicity (extremely high Mg:Ca ratio), and micronutrient toxicity (Mn, Fe, Ni…). Only serpentine-tolerant plants are able to survive in such high Mg conditions (Gao et al. 2015). To cope with Mg toxicity and avoid Ca deficiency, serpentine-tolerant plants have developed several physiological adaptations, including: (1) vacuole capacity to store excessive magnesium (Stelzer et al. 1990), (2) selective Ca uptake at the root and translocation to shoot levels, (3) restriction of internal Mg accumulation, and (4) Mg exclusion or sequestration at the root level (Alexander et al. 2007; Turner et al. 2010; O'Dell and Rajakaruna 2011).

Mg deficiency

Causes

Low Mg concentration in the soil

Highly weathered, acidic, and sandy soils are known to be Mg-deficient soils, since this nutrient is subjected to leaching in considerable amounts. Many findings were in accordance to indicate that magnesium is highly leached in these soils. According to Gransee and Führs (2013), magnesium leaching can reach up 25 kg ha^{-1}, while Mesić et al. (2007) explained that depending on many factors (crop type, drainage volume…), this value can be higher (45–70 kg ha^{-1}) in soils with limited fertility.

Calcareous soils

The presence of calcium and bicarbonate (HCO_3^-) with high amounts in calcareous soils is known to prevent Mg uptake by competing effect, resulting in magnesium depletion (Cakmak and kirkby 2008; Gransee and Führs 2013; Farhat et al. 2015b). It was also found that the formation of $MgCO_3$ in alkaline soils reduces Mg availability to plants (Broadley and White 2010).

Mg competition with Ca and K

It is well known that under Ca, Mg, or K deficiency, a relative or an absolute excess of the other cations can occur (Bergmann 1992). Indeed, these nutrients are strongly antagonistic and Mg is the least taken up nutrient (Voogt 1998). This poor ability of roots to take up Mg is attributed not only to root tissues but also to other plant organs (Mengel and Kirkby 2001). Schimanski (1981) supported these observations and reported that Mg availability can strongly modify Ca or K uptake, while Mg translocation can be restricted from roots to shoots by K and Ca. This phenomenon was observed in sunflower plants grown under insufficient Mg supply that showed an enhancement of Ca and K uptake (Lasa et al. 2000). Similar results were found by Hermans et al. (2004) who noticed in Mg-deficient sugar beet, a marked increase of calcium in roots and petioles and of potassium in all plant parts. These observations were in accordance to confirm the hypothesis of Peuke et al. (2002) who reported that a deficient nutrient enhances the uptake of other ones to compensate the charge balance of the omitted ion. In leaf mesophyll cells of bean plants, Mg uptake is facilitated by two systems: a non-selective ion channel that can transport calcium and potassium in both leaves and roots, resulting in an increase of their concentrations, while under Mg depletion conditions, another system (H^+/Mg^{2+} exchanger) is used (Hariadi and Shabala 2004). Hence, the competition for uptake was considered as a consequence of the lack of specificity of the individual uptake systems for each cation (Shaul 2002; Gardner 2003; Deng et al. 2006; Marschner 2012). This antagonistic effect was often observed in the presence of Mg, while a synergistic one was revealed by Narwal et al. (1985) and Ding et al. (2006) in the absence of Mg.

Antagonistic effects In rice plants subjected to increased K concentrations; both Mg concentrations and uptake were found to be reduced significantly in leaves and roots. However, no effect on Mg concentrations was reported under low K supply, which suggests that the antagonistic effect of K on Mg uptake was more marked than that of Mg on K uptake (Ding et al. 2006). These authors explained such results by a restriction of Mg translocation from roots to shoots. Farhat et al. (2013) noticed similar effects in safflower plants treated with excessive KCl concentration (60 mM KCl) that showed a significant decrease in Mg and Ca concentrations in all plant parts. This decrease was more pronounced in the case of magnesium under combined effects of high KCl concentration and low Mg supply (0.01 mM Mg). By contrast, no effect on potassium concentrations was noticed under Mg deficiency. According to Maguire and Cowan (2002), magnesium requires ion-specific proteins due to its specific characteristics. Thus, Mg has an ionic radius smaller than that of K while its hydrated radius is bigger. Another difference was found in the mechanisms involved in the transport of these two nutrients to roots (mass flow versus diffusion), resulting in a significant difference between K and Mg concentrations in soil solution mainly in the rhizosphere (Zhang and George 2002; Marschner 2012). In this context, Gransee and Führs (2013) reported that unspecific Mg transporters can be blocked by a high K availability in the soil/rhizosphere. For K uptake, two mechanisms were suggested: a "High-Affinity Transport System" (HATS) was proposed for a limited K concentration range, while a "Low-Affinity Transport System" (LATS) was suggested for over wide K concentration range (Britto and Kronzucker 2008).

Synergistic effects These effects were noticed by Ding et al. (2006) between K^+ and Mg^{2+} ions in rice plants. These authors found that Mg supply improved biomass yield and photosynthesis rate in rice plants fed with low K concentrations. However, no correction was noticed in chlorophyll concentrations. This supply of Mg was associated with an enhancement of K uptake and translocation from roots to shoots. The authors supposed that Mg could substitute K in some of its functions, which supports the hypothesis given by Bedi and Sekhon (1977) who suggested that some functions can be accomplished by one cation (Ca^{2+}, K^+, or Mg^{2+}) in the absence of another.

Symptoms

Being a key constituent of chlorophyll molecule, magnesium is associated with leaf yellowing in the form of interveinal chlorosis in older leaves under Mg-deficiency stress (Cakmak and Yazici 2010). The appearance of these symptoms is explained by the high involvement of magnesium in the synthesis of chlorophylls, the main pigments responsible for light harvesting in plants. Hence, magnesium depletion results in photosynthesis inhibition, carbohydrate accumulation in source leaves, and, consequently, in root growth reduction (Cakmak et al. 1994a, b), as well as in alterations in chloroplast ultrastructure (Fink 1993; Puech and Mehne-Jakobs 1997). The main aspects of Mg deficiency in plants reviewed in this study were summarized in Fig. 1. According to Paul and Foyer (2001), the disruption of carbohydrate balance between source and sink organs may accelerate leaf senescence due to an alteration of magnesium chelatase, an important enzyme responsible for inserting Mg into protoporphyrin IX, as the first step of chlorophyll biosynthesis (Walker and Weinstein 1991). An accumulation of protoporphyrin IX due to the alteration of magnesium chelatase may enhance the chlorosis development (Cakmak and Kirkby 2008), inducing an over-reduction of the photosynthetic electron transport and an over-production of ROS (Hermans et al. 2005; Cakmak and Kirkby 2008).

As recorded in many species, the exposure of *Sulla carnosa* plants to Mg-free medium (0 mM Mg) or low Mg concentrations (0.01 mM Mg) resulted in typical interveinal chlorotic areas affecting at a first step old leaves then progressing towards the younger ones and developing later into necrotic spots (Farhat et al. 2014). These observations were reported in a number of plant species grown under low Mg bioavailability, such as: *Arabidopsis thaliana* (Hermans and Verbruggen 2005) and sugar beet plants (Hermans et al. 2004). It was established that the appearance of Mg-deficiency symptoms is highly related to light intensity. Hence, high light intensity was found to increase the development of interveinal chlorosis due to an enhancement of damaging highly ROS generation in chloroplasts. Marschner and Cakmak (1989) found that the exposure of bean plants to high light intensity under sufficient Mg supply or to low light intensity (80 mmol photons $m^{-2}\ s^{-1}$) under Mg-deficiency conditions did not induce leaf chlorosis. By contrast, they noticed that Mg-deficient plants exposed to high light intensity (480 mmol photons $m^{-2}\ s^{-1}$) rapidly showed leaf chlorosis. According to these authors, such an aggravation of chlorosis by high light was not due to a decrease of Mg concentrations in leaves, but to a direct involvement of photooxidative destruction of chlorophyll and membrane lipids. Foyer and Noctor (2005) affirmed that magnesium deficiency may involve a programmed cell damage related to oxidative damage in chloroplasts. A similar effect was noticed with heat stress on Mg-deficient plants that were sensitive to high temperatures. Hence, wheat and maize plants exhibited interveinal chlorosis on their older leaves as grown under low Mg supply at 25 °C, and the effect was aggravated at 35 °C (Mengutay et al. 2013).

Photosynthetic activity alteration by Mg deficiency

Magnesium deficiency was found to adversely affect ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) involved in CO_2 fixation (Andersson 2008), which may explain the reduction of photosynthesis rate (Fischer 1997; Sun and Payn 1999; Ridolfi and Garrec 2000; Hermans and Verbruggen 2005). The inhibitory effect of magnesium deprivation on photosynthetic capacity and net CO_2 assimilation was noticed in several plant species (Terry and Ulrich

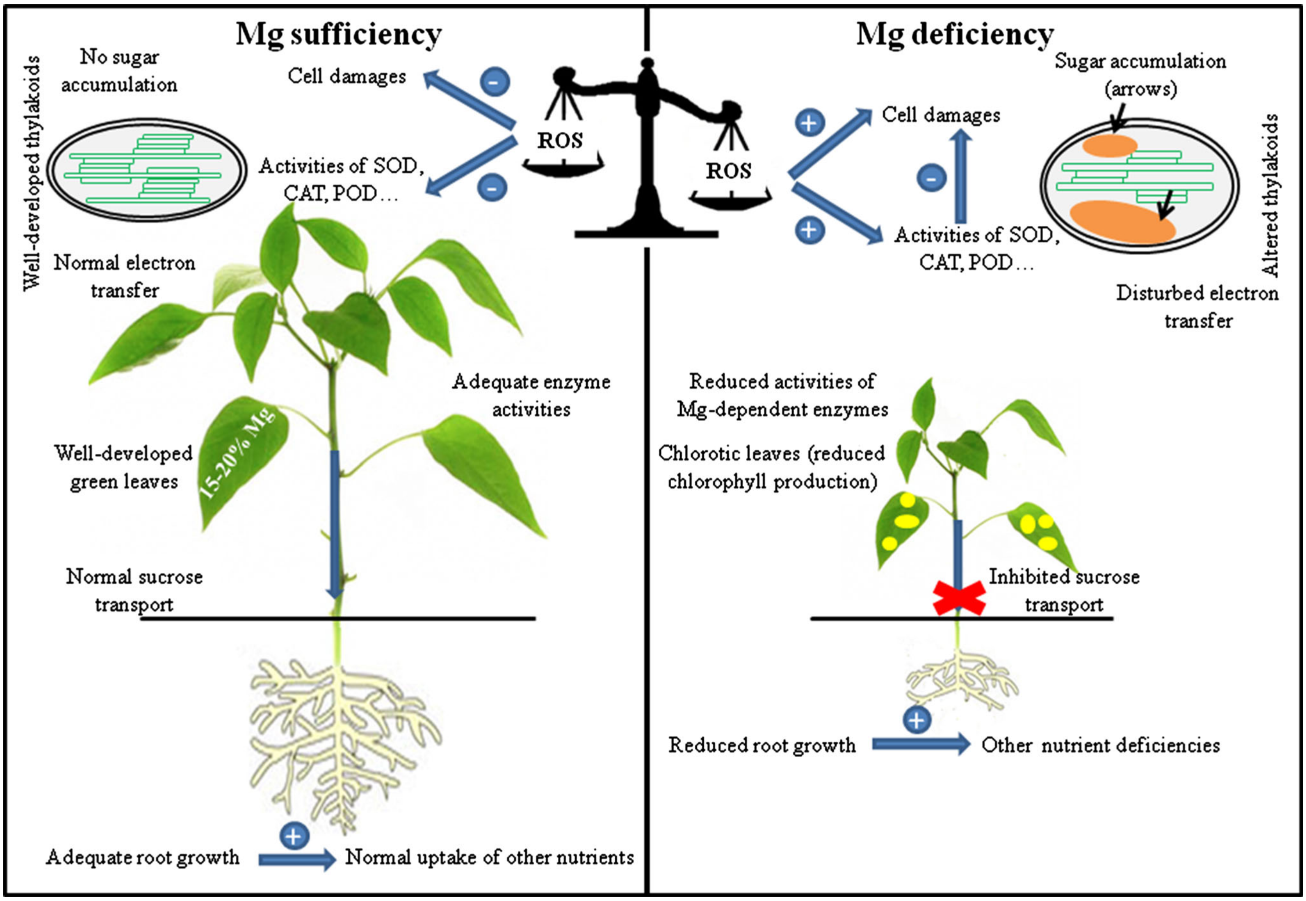

Fig. 1 Major effects of Mg deficiency in plants

1974; Fischer 1997; Sun and Payn 1999; Laing et al. 2000; Sun et al. 2001; Ridolfi and Garrec 2000; Hariadi and Shabala 2004; Hermans and Verbruggen 2005; Ling et al. 2009; Yang et al. 2012; Farhat et al. 2015a).

According to Ling et al. (2009), non-stomatal limitations might be the major factors determining the response of photosynthesis to Mg deficiency, since lower CO_2 assimilation is accompanied by an increase in intercellular CO_2 concentration. Indeed, Mg deficiency has been shown to induce an impairment of the linear photosynthetic electron transport (Hermans et al. 2004; Hermans and Verbruggen 2005; Tang et al. 2012; Farhat et al. 2015a), and this was suggested as the main factor contributing to decreased CO_2 assimilation (Tang et al. 2012; Yang et al. 2012). Under magnesium deficiency, the structure and the partial photochemical activities of PSI and PSII were found to be affected in some species. Hence, a decrease of Fv/Fm ratio (maximum quantum efficiency of PSII) was noticed in *Pinus radiata* (Laing et al. 2000), *Vicia faba* (Hariadi and Shabala 2004), and *Citrus* seedlings (Yang et al. 2012) under Mg-deficiency conditions. However, in Mg-deficient *Helianthus annuus* plants, this parameter (Fv/Fm) and other fluorescence parameters were not affected (Lasa et al. 2000). A reduction of Fv/Fm was also reported in *S. carnosa* plants grown at 0 mM Mg (data not shown). Similar results were found by Hermans et al. (2004) in sugar beet plants. These authors suggested that the decline of PSII activity is due to a loss of PSII antenna or, alternatively, to a change in photosystem stoichiometry in favor of photosystem I (PSI), resulting in an enhanced chlorophyll *a*/chlorophyll *b* ratio. Hence, an increase in chlorophyll *a*/chlorophyll *b* ratio is frequently observed under Mg shortage conditions (Lavon et al. 1999; Balakrishnan et al. 2001; Hermans and Verbruggen 2005). However, in some cases, this ratio was found to be decreased (Ayala-Silva and Beyl 2005) or unaffected (Ceppi et al. 2012). The reduction in LHCII amounts in Mg-deficient *Arabidopsis thaliana* leaves corresponds to a disorganization of thylakoid membranes (Hermans et al. 2004).

The measurements of the oxidation state of P700 ($P700^+$) (Klughammer and Schreiber 1991; Ivanov et al. 1998, 2006, 2012) in Mg-deficient leaves of *S. carnosa* showed a decline in the relative amount of oxidizable P700 ($P700^+$), which was concomitant with a marked reduction in the abundance of the antenna (Lhca1 and Lhca2) and core (PsaA and PsaB) polypeptides of PSI reaction centre (Farhat et al. 2015a). Hermans et al. (2004) explained such decrease in the total oxidizable P700 pool of Mg-deficient sugar beet plants by a loss of PSI centres, affecting the electron transport rate. A similar effect was observed in spinach plants subjected to combined deficiencies of Mg and S with a more reduced plastoquinone (PQ) pool (Godde and Dannehl 1994; Dannehl et al. 1996).

Photooxidative damage, ultrastructure alteration, and antioxidant responses to Mg deficiency

The appearance of chlorosis and necrosis is considered as a symptom of damages in chloroplast ultrastructure. This hypothesis was confirmed in several plant species by transmission electron microscopy. Chloroplasts become round and bigger due to an accumulation of oversized starch grains with disrupted thylakoids (Fink 1993; Puech and Mehne-Jakobs 1997; Farhat et al. 2014). Thus, a relationship between carbohydrate accumulation and leaf chlorosis appearance was often suggested. Wingler et al. (2005) explained chlorosis progression by a reduction electron transport under magnesium deprivation, which impairs CO_2 fixation and induces ROS generation. These species can seriously damage cell components, such as membrane lipids, proteins, and nucleic acids, resulting in metabolism disruption (Scandalios 2005). Malonyldialdehyde (MDA) accumulation was reported in *Mentha pulegium* (Candan and Tarhan 2003), *Zea mays* (Tewari et al. 2004), rice (Ding et al. 2008), and *S. carnosa* (Farhat et al. 2015b) plants as a general indicator of lipid peroxidation under low Mg availability conditions. However, it was established that under such conditions, the antioxidative defense system is stimulated to scavenge ROS that cause oxidative damages (Cakmak and Marschner 1992; Tewari et al. 2004, 2006; Riga et al. 2005; Yang et al. 2012). Hence, an induction of superoxide dismutase (SOD) activity was reported in various Mg-deficient plants, such as common bean (Cakmak and Marschner 1992), rice (Ding et al. 2008), and mulberry (Tewari et al. 2006), suggesting that under Mg deficiency, cells enhance their antioxidative defense system by initially increasing their SOD activities, since SOD is known to be the first enzyme involved in the protection of cells from the peroxidative attack of ROS (Bowler et al. 1992). The activities of other enzymes, such as catalase (CAT) and peroxidase (POD), may also be enhanced under such conditions. POD activity increase is explained by its high implication in the decomposition of H_2O_2 generated by SOD (Ding et al. 2008). This finding was concomitant with that found by Candan and Tarhan (2003) and Tewari et al. (2004, 2006) in Mg-deficient plants. However, it was noticed that CAT activity can decrease or remain constant in some cases (Tewari et al. 2004, 2006), indicating that severe deficiency could destroy the antioxidant system in plants. Kanazawa et al. (2000) found that a decline in SOD, CAT, and POD activities may also determine the sensitivity of plants to lipid peroxidation. Hence, when ROS production overcomes scavenging systems, the latter cannot provide a sufficient protection to membranes against photooxidation and oxidative stress occurs, resulting in a significant increase in MDA level (Ding et al. 2008).

Carbohydrate allocation disruption by Mg deficiency

In the majority of higher plants, the principal end products of leaf photosynthesis are starch and sucrose. Mineral deficiencies were supposed to affect carbohydrate partitioning (Ding and Xu 2011). The relationship between sugar partitioning and magnesium deficiency was studied by several authors (Hermans and Verbruggen 2005; Hermans et al. 2005; Cakmak et al. 1994a, b), who noticed that the most destructive effect of magnesium deficiency is sugar accumulation in source leaves, affecting later plant growth, photosynthetic activity, and leaf morphology. Thus, an accumulation of carbohydrates in source leaves and a reduction of root growth are considered as an earlier response to Mg deficiency, since it is involved in biomass formation and carbohydrate partitioning. In fact, carbohydrate accumulation together with the reduction of root/shoot ratio was reported in a variety of species under insufficient magnesium supply (Fischer and Bremer 1993; Cakmak et al. 1994a, b; Fischer et al. 1998; Mengutay et al. 2013). For this reason, chlorosis is not considered as suitable tool for an early diagnosis of Mg deficiency (Cakmak et al. 1994a, b; Ding et al. 2006), but as a late visible symptom (Gransee and Führs 2013). Farhat et al. (2014) observed a significant accumulation of soluble sugars (glucose, fructose, and sucrose) and starch in leaves of *S. carnosa* plants grown under absolute Mg deficiency (0 mM Mg) as well as under low magnesium availability (0.01 mM Mg), which correspond to the lowest pigment (Chl*a* and Chl*b*) concentrations. Ericsson and Kahr (1995) considered that sucrose accumulation seems to be the major growth constraint, especially for roots. Cakmak et al. (1994a, b) associated this increase of carbohydrates in *Phaseolus vulgaris* plants to a sensitivity of phloem sucrose loading under magnesium limitations. Sucrose and starch accumulation was also noticed in rosette leaves of sugar beet plants fed with deficient magnesium nutrient solution. This accumulation was accompanied by an impairment of their export from leaves to roots and resulted in an imbalance between sucrose accumulation and its utilization (Hermans et al. 2005). Rook et al. (2001) attributed this accumulation to an antisense expression of sucrose symporters, while Zhao et al. (2000) explained it by a co-suppression of the plasma membrane H^+-ATPase. According to some other authors (Ntsika and Deltrot 1986; Grusak et al. 1990; Paul and Foyer 2001), this increase is due to sink consumption reduction. Hence, being a mobile nutrient (80 % of magnesium is present in mobile forms), different hypotheses were given to explain the essential role of Mg in photosynthate export: (1) a structural damage and a destabilization in phloem tissue (Hannick et al. 1993), (2) a perturbation in the activity of sink organs, or (3) an impairment in phloem loading (Cakmak et al. 1994b; Hermans et al. 2005, 2006; Hermans and Verbruggen 2005). Cakmak and Kirkby (2008) reported that the third possibility may be related to a reduction of photosynthesis in Mg-deficient leaves. However, photosynthesis rate was found to be affected at later stages of this mineral deficiency. Thus, Mg starvation seems to have a direct functional and/or structural effect(s) on the phloem loading process of sucrose, confirming that photosynthesis alteration is not a sensitive indicator of Mg deficiency (Peaslee and Moss 1966). The importance of Mg in sucrose phloem loading was related to its interaction with nucleotidyl triphosphate (Mg^{2+}-ATP) fuelling the H^+-ATPases located in the plasma membranes of sieve tube cells. Therefore, under limited Mg concentrations, phloem loading inhibition into sink organs is explained by an impairment of H^+/ATPase activity in phloem companion cells (Bush 1989; Zhao et al. 2000). In fact, the binding of Mg by ATP is disrupted, which reduces the level of Mg-ATP complexes required by plasma membrane-bound ATPases. This results in the inhibition of photosynthate export via phloem (Hanstein et al. 2011; White 2012).

Concluding remarks

Despite Mg involvement in several vital functions in plants, it is still “forgotten” at the fundamental and applied levels. At the fundamental level, many mechanisms, including Mg uptake, translocation, transport mechanisms, and proteins mediating its transport in plants need to be more elucidated. At the applied level, the problem of Mg deficiency should be avoided to improve crop production and quality through the implication of this nutrient in soil fertilization, in particular, in the case of combined effects of magnesium deficiency and other abiotic stresses, such as heat and high light that are known to accentuate Mg deprivation symptoms.

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