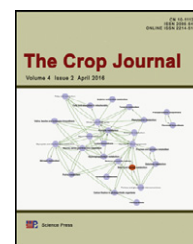
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Magnesium deficiency in plants: An urgent problem

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ABSTRACT

Although magnesium (Mg) is one of the most important nutrients, involved in many enzyme activities and the structural stabilization of tissues, its importance as a macronutrient ion has been overlooked in recent decades by botanists and agriculturists, who did not regard Mg deficiency (MGD) in plants as a severe health problem. However, recent studies have shown, surprisingly, that Mg contents in historical cereal seeds have markedly declined over time, and two thirds of people surveyed in developed countries received less than their minimum daily Mg requirement. Thus, the mechanisms of response to MGD and ways to increase Mg contents in plants are two urgent practical problems. In this review, we discuss several aspects of MGD in plants, including phenotypic and physiological changes, cell Mg^{2+} homeostasis control by Mg^{2+} transporters, MGD signaling, interactions between Mg^{2+} and other ions, and roles of Mg^{2+} in plant secondary metabolism. Our aim is to improve understanding of the influence of MGD on plant growth and development and to advance crop breeding for Mg enrichment.

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Abbreviations: ABA, abscisic acid; MGD, magnesium deficiency; ROS, reactive oxygen species; Cab2, chlorophyll a/b-binding protein gene 2; MgTRs, magnesium transporters; AtMHX, a Mg^{2+}/H^{+} exchanger; ART1, Al resistance transcription factor 1.

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1. Introduction

Magnesium (Mg) was recognized as an essential nutrient by 1925 [1]. For example, 60% or 25 g of Mg is located in adult bone, where it plays a central role in skeletal development [2]. Mg is essential for conformational stabilization of macromolecules such as nucleic acids [3], proteins [4], cell membranes, and walls [5]; maintenance of enzyme activities such as of H⁺-ATPase, kinases and polymerases [5–7]; and homeostasis of reactive oxygen species (ROS) under Al stress [8]. Mg also serves as a regulator of cation–anion balance in cells and as an osmotically active ion regulating cell turgor together with K [4,9]. Mg is particularly important to plants, with some 75% of leaf Mg involved in protein synthesis and 15–20% of total Mg associated with chlorophyll pigments [10], acting mainly as a cofactor of a series of enzymes involved in photosynthetic carbon fixation and metabolism [6,11,12].

However, plant Mg nutrition has been consistently overlooked by botanists and agronomists in past decades, unlike other ions such as iron (Fe), zinc (Zn), iodine (I) and selenium (Se) [13–15]. Surprisingly, people in many developed countries were commonly deficient in Mg [14,16], but this deficiency was not serious in developing or poor countries [17], indicating that loss of Mg by refining of food poses severe problems for human Mg uptake. For example, nearly 2/3 of adults surveyed in the USA and England received less than the estimated average daily requirement for Mg, and MGD leads to severe hypomagnesemia, manifested in such symptoms as sudden cardiac death, arrhythmia, muscle dysfunction, and attention deficit disorder [14]. The mean intake of Mg was 323 mg per day in men and 228 mg in women, values below the estimated indexes of 420 mg per day for men and 320 mg per day for women [18], and 10% of elderly women consumed less than 136 mg per day [19]. Thus, Mg contents in food crops and daily diets are an important problem in food quality and human nutrition [20], especially in regions where up to 75% of Mg intake daily is from cereals [21].

Pronounced declines of Mg concentration in cereal grains have been reported over the past several decades, likely owing to yield dilution coupled with the Green Revolution [22], and mimicking the changes in concentrations of Zn, Fe, I, and vitamin A [23]. For example, Mg contents in wheat dropped an average of 19.6%, from a mean range of 115–126 mg per 100 g dry weight (DW) before 1968 to 91–101 mg per 100 g DW after 1968 [24], and a similar trend was reported by other authors [25,26]. The declines in Mg, Zn, Fe, and I may also have some correlation with long-term unbalanced crop fertilization with nitrogen, phosphorus, and potassium (NPK) over the last decades. Grass tetany or paresis (milk fever) is a serious disorder in grazing animals, resulting from Mg decreases in grasses due to heavy application of potassium to soil [21]; K⁺ is an antagonist for Mg²⁺ absorption in plants. These results suggest that more attention should be paid to crop MGD and to the problems left to us by the Green Revolution. This review aims to summarize current knowledge about plant response to MGD, Mg²⁺ transporters, signal transduction, interactions between Mg²⁺ and other ions, and the role of Mg²⁺ in plant secondary metabolism.

2. Many stress factors limit magnesium availability by plants

The Mg requirement for optimal plant growth is 1.5–3.5 g per kg in vegetative parts, and Mg concentrations in soil solutions lie between 125 μmol L⁻¹ and 8.5 mmol L⁻¹, values sufficient to support plant growth [4,16]. Although lower Mg appears under some conditions, such as in acidic soils with low cation exchange capacity, about 70% of the potentially arable land on earth is acidic. High rainfall in tropical regions leads to Mg leaching [27,28], aluminum toxicity [29], heat stress [30], droughty soil [27], and high levels of competing elements, such as K, calcium (Ca), ammonium (NH₄), and sodium (Na). In particular, long-term unbalanced crop fertilization (NPK) leads to Mg²⁺ depletion, cation competition, and subsequent Mg²⁺ leaching [31]. These changes result in the decrease of Mg²⁺ availability to plants, lower accumulation of Mg in seeds, marked inhibition of plant growth, acceleration of aging, and reduced productivity and quality in agriculture, horticulture, and forestry [32]. These consequences suggest that the chemical and physical characteristics of soils are among the most important factors in Mg²⁺ availability by plants.

3. Changes induced by MGD in plants

Generally, MGD results in shorter roots, smaller shoots, and necrotic spots on leaves [7,33,34], owing mainly to abnormal physiological processes reflected in impaired carbon metabolism and decline of chlorophyll and carbon fixation (Fig. 1). In a transcriptomic analysis, a far greater number of early response genes was observed in roots than that in leaves to Mg deprivation [35]. The transcript patterns of one fifth of the genes in leaves and half in roots were restored to the initial patterns after Mg supplementation of the nutrient solution for 24 h. MGD-responsive genes in leaves changed gradually after 8 h and even after one week [34]. Mg in shoots declined quickly within one day after the removal of Mg [7,35–37], suggesting that shoot and leaf are secondary response organs following changes in Mg level.

MGD disrupts the loading of sucrose into phloem (Fig. 1), resulting in carbon accumulation in source leaves. Resupply of Mg rapidly enhanced sucrose export to phloem from source leaves [4,7]. Such rapid recovery of sucrose export was found under both dark and light conditions, indicating that enhancement of sucrose export after Mg resupply is associated not with photosynthesis but only with Mg availability. A decline in Mg-ATP concentration at the phloem-loading sites may be the major reason for inhibition of sucrose transport from Mg-deficient source leaves [11] and is analogous to sucrose accumulation in leaves under K and Zn but not P deficiency [4]. Sucrose loading into phloem is catalyzed by an H⁺/sucrose co-transporter (Fig. 1), whose activity requires a proton gradient maintained by an H⁺-ATPase located in the plasma membranes of sieve tube cells [11]. Growing evidence indicates that Mg-ATP is a major complex of ATP in cells and is essential for the proper functioning of H⁺-ATPase [38]. *BvSUT1*, a phloem-specific proton-sucrose symporter located in companion cells of the vascular system, is induced by MGD in sugar beet leaves [39,40].

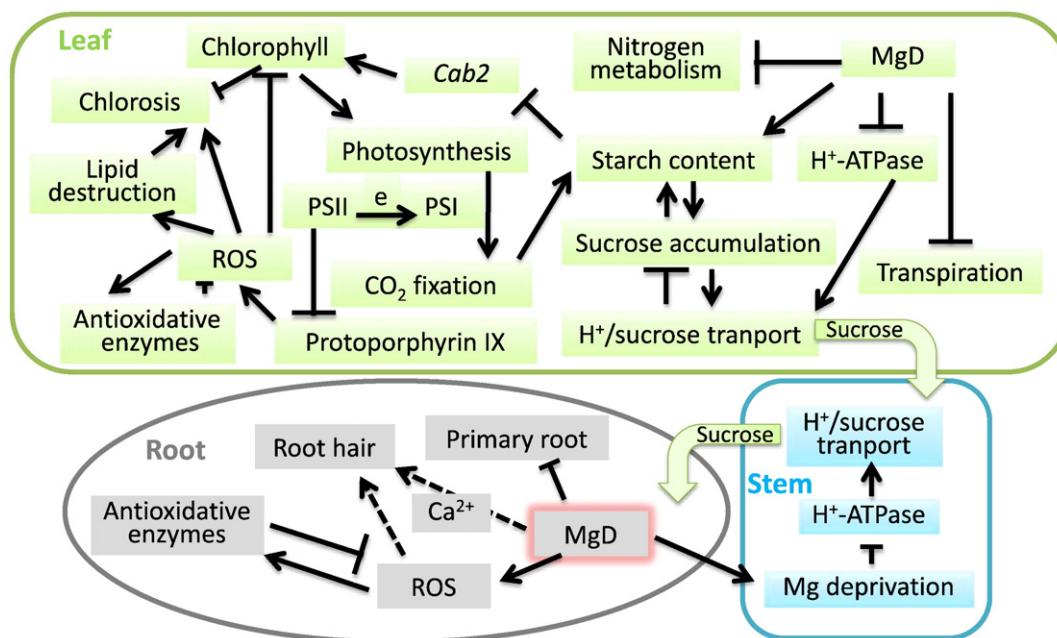


Fig. 1 – Potential processes in plant response to magnesium deficiency (MGD), based on references cited in this review. Solid arrows indicate activity of downstream steps, blocked lines show inactivity of downstream steps, and broken lines represent possible processes. ROS, reactive oxygen species; Ca, calcium; Cab2, chlorophyll *a/b*-binding protein gene 2; PS, photosystem; e, electron.

Mg²⁺ acts as an enzyme activator or cofactor in carbohydrate metabolism, so that MGD inhibits these enzyme activities and further leads to carbon accumulation in source leaves, such as fructose-1, 6-bisphosphatase (FBPase), glutamate synthetase, UDP-D-, ADP-D-, G6PD-glucose pyrophosphorylase, and UDP-D-glucuronic acid pyrophosphorylase [7]. Overaccumulation of carbides in leaves leads to feedback inhibition of the photosynthesis rate [41] and reduces chlorophyll concentration by repression of *Cab2* (chlorophyll *a/b*-binding protein gene 2, which encodes Chl *a* and *b* proteins) [7].

Impairment of photosynthetic CO₂ fixation also leads to an accumulation of unused electrons in the chloroplast, resulting in ROS generation and photo-oxidative damage to chlorophyll and chloroplast membrane lipids (Fig. 1). Thus, MGD symptoms such as leaf chlorosis, are aggravated by high light intensity [13]. This process is due to the inhibition of the transfer of excitation energy (or electrons) from chl-*a* of PSII to chl-*a* of PSI in chloroplast [42], or due to low content of PSI [43]. The electrons are transferred to protoporphyrin IX, probably in association with the light-dependent generation of ROS, resulting in leaf chlorosis following the overaccumulation of protoporphyrin IX in tissues (Fig. 1), especially under MGD and high light intensity. In addition, MGD may reduce Mg chelatase (MgCH) activity in the presence of limited ATP and Mg²⁺. MgCH catalyzes the ATP-dependent insertion of Mg²⁺ into protoporphyrin IX to produce Mg-protoporphyrin IX, the first committed step in the chlorophyll biosynthetic pathway [44]. In this manner, protoporphyrin IX is overaccumulated in cells.

MGD also activates antioxidative defense enzymes in some plant species [34,37,45]. The key antioxidant molecules (dehydroxyascorbate and oxidized glutathione) were markedly increased within 1 week in *Arabidopsis* with MGD treatment

[34]. Generally, leaf chlorosis is observed first in older leaves in response to MGD, and is interpreted as the re-translocation of Mg²⁺ from older to younger leaves [4]. A decrease in transpiration occurs prior to sugar accumulation and chlorosis in rice under MGD conditions [46]. These results indicate that plant MGD-response systems are complex and that many signal transduction pathways are unknown.

Besides the impairment by MGD of carbon metabolism in source leaves, nitrogen (N) metabolism is also damaged. For example, lower N was reported in longan leaves [47] under MGD treatment, and some enzymes of N metabolism were inhibited in spinach by MGD, including N reductase, glutamate synthase, glutamate dehydrogenase, urease, glutamic-pyruvic transaminase, and glutamic-oxaloacetic protease transaminase [48]. More than 10 N transporters were induced by MGD in *Arabidopsis* in our latest research (unpublished data). However, little is known of the effects of MGD on N metabolism.

4. Magnesium transporters mediate Mg²⁺ homeostasis in plant cells

Understanding of Mg²⁺ homeostasis in plant cells has been advanced by the discovery of *Arabidopsis* Mg²⁺ transporters (MgTRs) [49,50]. AtMHX (an Mg²⁺/H⁺ exchanger) is the first cloned MgTR in plants [51], is located in the vascular system (Fig. 2), and adjusts osmotic potentials especially in phloem cells [52]. The results of AtMHX's cis-regulon analysis [52–54] and overexpression of AtMHX [55,56] indicate that AtMHX maintains metal and proton homeostasis in cells or participates in photosynthesis.

Most known MgTRs are CorA transporters and harbor a conserved Gly-Met-Asn (GMN) tripeptide motif at the end of

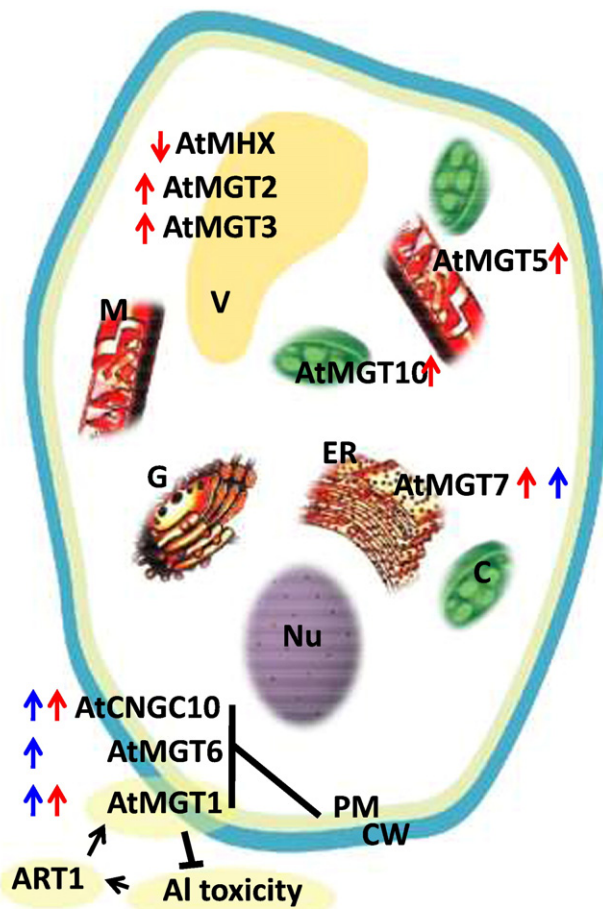


Fig. 2 – Subcellular localization of magnesium transporters in *Arabidopsis* and changes in their expression levels caused by magnesium deficiency (MGD), magnesium toxicity (MgT), and aluminum (Al) toxicity. Red arrows indicate transcriptional changes of magnesium transporter genes induced by MgT, blue arrows show transcriptional changes (upward arrow denotes upregulation and downward arrow downregulation) of magnesium transporter genes by MGD, black arrows represent activity of genes, and a blocked line denotes inhibition. ER, endoplasmic reticulum; V, vacuole; G, Golgi apparatus; PM, plasma membrane; CW, cell wall; Nu, nucleus; M, mitochondria; C, chloroplasts; CNGC10, cyclic nucleotide gated channel 10; MHX1, magnesium exchanger 1; MGT, magnesium transporter; ART1, Al resistance transcription factor 1.

the first transmembrane domains [49]. Ten *CorA* superfamily *AtMGT* (Mg Transporter) genes, with the exception of the pseudogene *AtMGT8* [57,58], are clustered into high-affinity (*AtMGT1* and *AtMGT10*), low-affinity (*AtMGT3*, *AtMGT7* and *AtMGT9*), and dual-affinity (*AtMGT5*) members by their affinities for Mg^{2+} transport, as confirmed using bacteria or yeast mutant systems [49]. They are considered the primary Mg^{2+} transport system in plants and play the major roles in Mg^{2+} uptake, distribution, and homeostasis in cells [15], deduced from their subcellular locations: plasma membrane, endoplasmic reticulum, vacuole, mitochondrion, and chloroplast [59,60] (Fig. 2). However, only plants with silencing of *AtMGT6*

[60], overexpression of *AtMGT7* [59] and *AtMGT1* [61], and double (*AtMRS2-1/10*) or triple (*AtMRS2-1/5/10*) mutations [62] showed phenotypic changes in response to MGD. Surprisingly, the growth retardation of double or triple mutants with MGD treatment could be reduced by reduction in Ca^{2+} concentration [62], although the exact mechanism is unknown. *AtMGT7* showed high expression in roots. Knockout lines of *AtMGT7* showed reduced growth retardation under low Mg, suggesting that *AtMGT7* is involved in Mg uptake; however, *AtMGT7* was localized to the endoplasmic reticulum [59]. Rice *OsMGT1* was regulated by an Al-responsive transcription factor *ART1* (Al resistance transcription factor 1) [63] (Fig. 2), and *Arabidopsis* plants with overexpression of *AtMGT1* and *OsMGT1* were resistant to Al toxicity [29,61]. Although *AtMGT1* is localized in the plasma membrane, it is expressed in root hairs, root elongation zones, vascular tissues, and trichomes of adult leaves [59]. These findings indicate that Mg transport by *MGT1* is induced by Al^{3+} and not by MGD, as confirmed by the observation that plants with the increased Mg^{2+} in the cytosol are resistant to Al^{3+} toxicity [8]. *AtMGT6*, another plasma membrane Mg^{2+} transporter, mediates Mg^{2+} uptake by roots, especially under a low- Mg^{2+} environment [60]. *AtMGT2* and *AtMGT3* are involved in Mg partitioning in *Arabidopsis* mesophyll vacuoles and are localized to the tonoplast [64], consistently with their expression in both rosette and cauline leaves [59], as is *AtMHX* [51], which maintains cation balance in the vacuole. Some *AtMGTs* [65] and *AtMHX* [66] colocalize with major quantitative trait loci (QTL) thought to affect Mg concentration in *Arabidopsis* seeds. Mg contents increase in phloem during grain loading in common wheat [67]. The expression levels of these *MgTRs* change little in transcriptomic analysis, but many are activated by Mg toxicity [68]. *AtCNGC10*, the latest discovered plasma membrane *MgTR*, mediates Mg^{2+} uptake and long-distance transport and may be involved in Ca^{2+} , K^{+} , and Na^{+} (under salinity) transport in *Arabidopsis* [50]. *AtMGT5* and *AtMGT9* are essential for pollen development and male fertility [69,70], *AtMGT5* is localized in mitochondria [70]. *AtMGT10* is localized in the chloroplast envelope membrane system and is expressed in the rosette leaves and vascular tissues of cauline leaves [59,71], indicating a possible function in Mg^{2+} translocation into chloroplasts [71]. Two members of the class II HKT transporters in rice also transported Mg^{2+} and Ca^{2+} , but these processes could be impaired by K oversupply [72]. These reports suggest that other transporters also play important roles in plant response to MGD. Our latest research (unpublished) supports this suggestion.

5. Signaling response to MGD in plants

Signal transduction responding to MGD in plants has been little investigated, although there are reports of expression changes of many genes under MGD, including genes governing ethylene biosynthesis, ROS detoxification, photoprotection, ABA response, and circadian rhythm [34,35,37,52]. Niu et al. [37] presented evidence that ROS and cytosolic Ca^{2+} are signaling factors responding to MGD, in agreement with a previous hypothesis that antioxidation is an early response to MGD induced by ROS [11,34]. In addition, ROS may inactivate

photosynthetic and starch metabolic enzymes under MGD [7], such as ribulose-1,5-biphosphate-carboxylase (RUBISCO), which is very sensitive to ROS under low temperature and high light conditions [73]. Hermans et al. [35] found no change in ABA content in plants treated with MGD, in contrast to those subjected to Mg toxicity (MGT), ABA levels increased in both roots and shoots [68,74], although Hermans et al. [35] observed that half of the upregulated MGD response genes in leaves were ABA-responsive. These findings suggested that the factors responding to ABA are involved in MGD signaling independently of ABA. MGD-treated plants produced twice as much C₂H₄ gas as control plants, and the expression levels of several gene encoding enzymes (ASC2; 7; 8; 11) in the C₂H₄ biosynthetic pathway were enhanced accordingly [34], suggesting that ethylene plays a key role in response to MGD. Our unpublished data also indicate that more than 15 ethylene response transcription factors are induced by MGD. Abscisic acid (ABA) and auxin are also involved in regulation of AtMHX [52] and the cis-regulon is in its first intron [52–54]. However, these findings are too fragmentary to reveal the signaling pathway. The rapid development of genomic, transcriptomic, non-coding RNA, and proteomic technologies may help us to identify MGD signaling pathways in plants.

6. Interaction between magnesium and other ions

There are interactions between Mg²⁺ and other ions. High K⁺ and Ca²⁺ result in lower Mg availability to plant roots [28,75]. Several AtMGT genes have shown higher expression in low-Ca²⁺ solution, but this expression was not observed in double mutant (*cax1/cax3*, Ca transporter) plants under MGD conditions [34,35]. These findings suggest that plant cells compensate for low Ca²⁺ by increasing Mg transporter activity, whereas high Ca²⁺ inhibits Mg²⁺ availability to plants. K⁺, in addition to competing for apoplast binding sites [76], possibly competes for transporters. For example, two members of class II of K⁺ transporters (*OsHKT2*; 4 and *TaHKT2*; 1) also transported Mg²⁺ in *Xenopus laevis* oocytes [72]. Mg²⁺ uptake in leaf mesophyll cells of broadbean was facilitated by two systems, a nonselective ion channel and an H⁺/Mg²⁺ exchanger (MHX). The latter acts at lower Mg²⁺ concentrations, and the nonselective channel system is also capable of K⁺ and Ca²⁺ transport [77]. These findings may explain why high K⁺ inhibits Mg²⁺ uptake. Under MGD conditions, cerium (a rare earth) ion promotes the synthesis of chlorophyll and photosynthetic pigments, increases activities of two key enzymes in CO₂ assimilation and the antioxidative defense system, increases the expression of Rubisco large subunit (*rbcl*), small subunit (*rbcs*), and activase subunit (*rca*), but decreases malondialdehyde and ROS in spinach [44,78–80]. These results suggest that cerium plays a role similar to those of Mg, but the mechanisms are unclear. Lanthanum shows a behavior similar to that of cerium in spinach in response to MGD [81].

Inhibition of plant growth and development by many toxic heavy ions and Al³⁺ can be reduced by addition of high Mg²⁺. For example, Cu²⁺ toxicity is alleviated by Mg²⁺ treatment in barley [82], wheat [83], cowpea [84], and grapevine [85,86], but not in sugar beet [87] and lettuce [88], suggesting that the influence of Mg²⁺ on Cu²⁺ phytotoxicity depends strongly on

plant species. Application of high Mg²⁺ alleviates the growth inhibition of mustard plants subjected to cadmium (Cd) toxicity [89]. Pretreatment of plants with Mg starvation prevents the bleaching of young leaves caused by high Cd in *Arabidopsis* [90] and rice [75]. Pretreatment of Mg starvation may increase the anti-oxidative capacity and modulate Fe homeostasis, and/or promote cytosolic efflux transport or vacuolar storage of Cd to reduce Cd-induced injury [90]. Plants with overexpression of Mg²⁺ transporter genes (*AtMGT1* and *OsMGT1*) in tobacco [61] and rice [29] are resistant to Al³⁺ stress (Fig. 2), and similar results were reported for soybean [93], rice [29], *Arabidopsis* [90], and rice bean [94] treated with high Mg²⁺ and Ca²⁺ under Al³⁺ toxicity conditions [8,27,91,92]. It is generally considered that Al³⁺ and Mg²⁺ ions compete for membrane transporters and metal binding sites of enzymes [92,95]. Al³⁺ toxic soils inhibit Mg²⁺ absorption by plants [29], but Al³⁺ toxicity can be alleviated by high Mg²⁺ via reduction of Al³⁺ saturation of apoplasmic binding sites, decreasing Al³⁺ activity at the root cell plasma membrane surface [95], and/or increasing the exudation of Al-induced organic acids by plant roots, such as in soybean [93], rice bean [94], and broad bean [96]. Interestingly, a 2.3-fold variation in shoot Mg²⁺ concentrations in various genotypes of *Brassica oleracea* has been reported, and variation in tissue Mg²⁺ concentration is highly heritable [97], giving promise of breeding crops with Mg enrichment, and increased tolerance to Al³⁺ and H⁺ toxicity. Low pH (pH < 4.5, high H⁺) inhibits Mg²⁺ uptake in plants [98,99], and acid soils support higher leaching rates of Mg²⁺ and higher concentrations of toxic ions such as Al and manganese [27,29]. Increasing NO₃⁻ supply increases the uptake of Mg²⁺ but decreases its translocation [100], while increasing Mg²⁺ supply can reverse ammonium toxicity [101]. These results indicate the complexity of the interactions between Mg²⁺ and other ions.

7. Secondary metabolism in plants affected by Mg²⁺

Mg²⁺ also affects secondary metabolism in plants. MGD increases cardenolide production in callus cultures of *Digitalis davisiana* Heywood, *D. lamarckii* Ivanina, *D. trojana* Ivanina, and *D. cariensis* Boiss [102], phenolic compounds [103], and putrescine accumulation [104]. Putrescine accumulation in cells is a universal response to stress in plants. Anthocyanins in red grape cell suspension culture are increased and their catabolism is decreased under Mg²⁺ treatment [105], as is in several ornamental plants by spraying the foliage or by drenching pot plants with Mg²⁺ solution [106,107]. Aster plants with Mg²⁺ treatment increased pigment concentrations without inducing the activity of key enzymes of the anthocyanin biosynthetic pathway in flower buds [107]. A similar effect was observed in *Anigozanthos*, *Limonium*, *Gypsophila*, and *Aconitum* flowers [106]. However, little is known about Mg's roles in plant secondary metabolism.

8. Conclusions

Magnesium deficiency in plants is becoming an increasingly severe problem with the development of industry and agriculture

and the increase in human population. However, little is known today about the response mechanism. People have suggested that the discovery of Mg^{2+} transporters in plants might be 'the tip of the iceberg' [15], and will help us to understand plant response profiles to MGD. However, studies in the last decade have shown that most known Mg^{2+} transporters govern Mg^{2+} homeostasis only in plant cells, tissues and organs, with only AtMGT6 [60] and AtCNGC10 [50] in roots possibly involved in Mg^{2+} absorption from the rhizosphere under MGD. Both genotypic analysis of *B. oleracea* [96] and transcriptomic analysis of *Arabidopsis* [34,35] suggest that complex systems in plants and other unknown transporters play key roles in MGD response. Interactions between Mg^{2+} and other ions, including toxic and nutrient ions, also appear complex under MGD conditions [28] such as Mg deprivation and competitive Mg^{2+} deficiency. The large phenotype changes and signal transduction responses to MGD in plants (Fig. 1) increase the difficulty of explaining the mechanisms. Mg content in seeds declined markedly after 1968 [24–26] in parallel to the Green Revolution and the history of heavy chemical fertilization in agriculture [21,22]. Consequently, most people absorb lower Mg from cereals than the estimated indexes [14,16,18,20,21]. Thus, MGD in plants is an urgent problem. Some questions must be in the coming years: (1) Which transporters are most responsible for Mg^{2+} transport from the rhizosphere to root cells? The known Mg^{2+} transporters are not sufficient to respond to Mg deficiency in plants. (2) What signaling is specific to MGD, what are the signal receptors and factors, and what are the interactions between phytohormones and their factors in signal transduction? (3) Can we select cereals with high Mg enrichment on Mg-deficient soils? (4) Are there novel factors involved in the response to Mg deficiency in plants? These could include microRNAs, which participate in many stress responses, including nutrient stresses.

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