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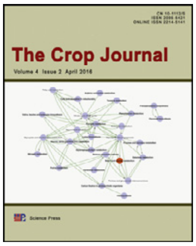

Magnesium deficiency in plants: An urgent problem

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ARTICLE INFO

Article history:
Received 25 August 2015
Received in revised form
18 November 2015
Accepted 26 November 2015
Available online 11 December 2015

Keywords:
Plant
Magnesium deficiency
Magnesium transporter
Interaction
Signaling

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.

Contents

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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Peer review under responsibility of Crop Science Society of China and Institute of Crop Science, CAAS.

http://dx.doi.org/10.1016/j.cj.2015.11.003

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 Mg^{2+} 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, Mg^{2+} transporters, signal transduction, interactions between Mg^{2+} and other ions, and the role of Mg^{2+} 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 (NH_4), and sodium (Na). In particular, long-term unbalanced crop fertilization (NPK) leads to Mg^{2+} depletion, cation competition, and subsequent Mg^{2+} leaching [31]. These changes result in the decrease of Mg^{2+} 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 Mg^{2+} 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].