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The Nutrient Magnesium in Soil and Plant: A Review

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This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Magnesium is the third most abundant structural metal in the Earth's crust and is found in many rock minerals and in seawater. In the soil, it appears in the ionic form Mg^{2+} , in solution and as an exchangeable cation. After absorption, Mg^{2+} is transported from the roots to the aerial part through the interior of the plant, giving this process the name of translocation. In plants, magnesium plays a fundamental role for growth and development, participating in a series of important processes for the metabolism of the plant, such as the constitution of the chlorophyll molecule, in addition to acting as an enzymatic activator. Thus, given the importance of the magnesium nutrient, the objective of this review is to present the main aspects of this nutrient in the soil and the functions performed in plants.

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1. INTRODUCTION

For the plant to complete the growth, development and reproduction phase, it is necessary to supply adequate levels of water, light and nutrients.

Nutrients are classified based on direct and/or indirect criteria of essentiality for plant growth. Thus, a nutrient is considered essential when its absence prevents the plant from completing its life cycle. Based on this concept and on their relative concentrations found in plant tissues, mineral elements are further classified into macro and micronutrients. The macronutrients are nitrogen (N), potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), sulfur (S), and silicon (Si). While chlorine (CI), iron (Fe), boron (B), manganese (Mn), sodium (Na), zinc (Zn), copper (Cu), nickel (Ni) and molybdenum (Mo) are listed as micronutrients.

Among the macronutrients, magnesium stands out for actively participating in a series of vital processes with a structural function in plant metabolism, mainly as a central and essential component of the chlorophyll molecule framed as the main function of this element, in addition to acting as an enzymatic activator.

Thus, the objective of this work is to provide information about magnesium considered by the literature as a secondary macronutrient, with a brief history of its origin, its main functions in plant metabolism, forms of absorption, transport and redistribution, as well as the symptoms of deficiency and toxicity for the main crops of commercial interest.

2. MAGNESIUM

Magnesium (Mg) was discovered in 1808 by Sir Humphrey Davy. It is a metallic chemical element, symbolized by the acronym Mg, placed in group IIA of the periodic system, atomic number 12, valence 2 and atomic mass 24.312 g/mol. its coloration is white silver being considered very light. It has a relative density rated at 1.74 g/ml, boiling point 1107°C, melting point 650°C and density of 1740 kg/m³. Among other elements, it is known as the lightest structural metal in the industry, due to its low weight and ability to form mechanically resistant alloys [1].

It is a very abundant element in nature, and is found in imported quantities in many rock minerals, and in sea water. It is the third most abundant structural metal in the earth's crust, surpassed only by aluminum and iron. Furthermore, it is the eighth mineral element considerably found in the earth's crust and its content in soils varies from 0.1% in coarse textured soils, sandy and in humid regions to up to 4% in fine textured soils in arid or semi-arid regions [2].

The main natural sources of Mg are eruptive, sedimentary and metamorphic rocks [3]. It originates from the weathering/decomposition of rocks containing primary minerals such as dolomite and silicates (hornblende, olivine, serpentine and biotite) and is also part of the structure of secondary clay minerals such as chlorite, illite, montmorillonite and vermiculite [2] The more weathered the soil, the less occurrence of these minerals, until only exchangeable Mg remains adsorbed to colloids and components of soil organic matter.

In the cerrados of Brazil, about 90% of the oxisols and argisols suffer from Mg deficiency, as a result of the high degree of weathering and leaching. The amounts lost depend on the interaction of several factors: Mg content in the soil, H^+ and Ca^{2+} concentrations, weathering rate, leaching intensity and removal by plants [2].

Soil magnesium content varies depending on parent material, clay type and soil texture. For example, peridotite and dolomite basaltic rocks and chlorite, vermiculite and illite clays are rich in magnesium [4].

In agriculture, it is mainly supplied in the form of limestone, but it can also be supplied to plants as magnesium sulfate and oxide and magnesite. The latter being the main natural source of magnesium. Its chemical formula has 47.8% MgO and 52.2% CO₂. It is a noble raw material, widely used to obtain metallic magnesium and some magnesium compounds, used in the pharmaceutical, chemical and refractory industries [5].

As mentioned, Mg is considered a secondary macronutrient in fertilization due to its applied amount [6]. The Mg requirements of crops are relatively low, in the order of 10 to 40 kg/ha for most cases, normal levels in leaves vary little between species, being generally in the range of 0.2 to 0.4%. According to Malavolta [3], the need for Mg for optimal plant growth is in the range of 1.5 to 5 dag kg-1 of dry matter of the diagnostic leaf.

As magnesium is not a nutrient normally used in fertilizers, but in liming, there is not much data on crop responses to magnesium. However, deficiencies have occurred with a certain frequency in acid soils, being aggravated in cultures that receive high potassium applications [7].

It is a constituent mineral of chlorophyll and consequently is actively involved in photosynthesis. Most of the magnesium in plants is found in chlorophyll, but seeds are also relatively rich, although grain-producing crops such as corn have low levels of this nutrient. Magnesium also helps with phosphate metabolism, plant respiration, and activation of various enzyme systems.

In summary, magnesium plays a fundamental role in the growth and development of plants. Thus, it is important to know magnesium in the plant system, in all its "compartments" that the nutrient travels through from the soil solution, root and part of the area, to its incorporation into an organic compound or as an enzymatic activator, performing vital functions to allow the maximum accumulation of dry matter in the final agricultural product [8].

3. MAGNESIUM DYNAMICS IN THE SOIL-PLANT SYSTEM

Magnesium (Mg) in soil is present in the ionic form Mg^{2+} , in solution and as an exchangeable cation. It participates in the structure of micas and clay minerals of the 2:1 type, which are found in less weathered soils, and it is also possible to find other minerals with this element [9].

In soils with good drainage, the exchangeable levels of calcium (Ca) predominate in the sum of bases, followed by magnesium with much lower levels and later followed by potassium (K). Magnesium can appear in soil as insoluble carbonates, in calcareous soils or in soils that have recently been limed. In general, the supply of magnesium to crops depends on the Mg content and its availability in the soil [9].

As with K and Ca, Mg appears in the soil, according to Malavolta [10], in different forms:

Primary minerals: silicates, mainly have structural magnesium, as is the case of pyroxenes, amphiboles, olivine, and tourmaline, muscovite and biotite also have Mg.

- Carbonates and sulfates: dolomite, CaCO3MgCO3, dolomitic and magnesian limestones, magnesite (MgCO3) may occur in layers in arid and semi-arid regions, epsomite (bitter salt, MgSO47H2O) may appear in the soil;
- Secondary minerals: Mg can enter the composition of some clays, such as montmorillonite, illite, and chlorite, by replacing octahedral aluminum; vermiculite, a product of the hydrothermal weathering of micas, has Mg which displaces K;
- Organic matter: existence of Mg present in organic compounds.

Higher levels of magnesium are found in clayey soils, as this element is present in easily weathered ferromagnesian minerals, such as: biotite, serpentine, hornblende and olivine. Mg also occurs in secondary minerals, which include chlorite, vermiculite, illite, montmorillonite. Some soils contain Mg in the form of magnesite (MgCO3) or dolomite (CaMgCO3). In arid and/or semi-arid regions, soils can contain large amounts of Mg, such as epsomite (Mg SO47H2O) [9].

The distribution of Mg in soils can be considered similar to that of K and Ca and can be divided into the following forms: non-exchangeable or fixed, exchangeable and soluble. The major fraction of Mg in soil is in the non-exchangeable form, which includes all of the Mg in the primary minerals and most of the Mg in the secondary minerals. The exchangeable Mg is of the order of approximately 5% of the total Mg. This fraction together with soluble Mg is of the utmost importance for the supply of this nutrient to plants [11].

In acidic soils of humid regions, Mq^{2+} is the third most abundant cation in the exchange complex, after Ca²⁺ and H⁺, in soils of semi-arid regions, it comes right after $Ca²⁺$, except in alkaline soils, where it loses place to $Na⁺$. In acid soils, it is possible that there is competition between H+ and Al3+ in the absorption of Mg^{2+} , while competition with Ca+ can occur where high doses of limestone are applied. Thus, by lowering or raising the pH, the absorption of $Mg²$ decreases due to competition from H^+ or Al^{3+} or Ca^{2+} [9].

Soil Mg depends on soil texture and organic matter content, both of which are responsible for soil cation exchange capacity. With equal amounts of exchangeable Mg, the solution concentration is usually higher in sandy soils than in soils with a high clay content. This can be explained by the fact that soils with a high clay content have a greater adsorbent capacity than sandy soils. However, the release of Mg from the exchangeable complex in clayey soils is generally lower than the demand for crops, requiring large amounts of available Mg for optimal plant growth [2].

The behavior of the ion in the soil depends on its characteristics that determine its greater or lesser mobility. Thus, mobility means how much a certain ion moves in the soil [7].This greater or lesser mobility in the phloem has practical relevance, since when there is a decrease in the supply of nutrients from the soil to the plant, the symptoms appear in:

- 1. Mobile elements old leaves in the case of Mg.
- 2. Little mobile elements young leaves.
- 3. Immobile elements young leaves and apical meristems.

In the same way as other nutrients, the increase in the pH value of the soil, close to 6.5, allows greater availability of Mg in the soil [12].

3.1 Absorption

Plants absorb magnesium exclusively from soil solution in the form of Mg^{2+} in which Mg remains in the exchangeable fraction of the soil, adsorbed to negatively charged colloids, and is transported to plant roots.The first step for the element to be absorbed is to come into contact with the root, which can be established by three different processes, root interception, by diffusion or by mass flow [7].

The latter is the process responsible for the greater proportion of the contact of the divalent cations (Ca^{2+} and Mg^{2+}) with the root, that is, the movement of Mg^{2+} from the soil to the plant roots is mainly due to the mass flow mechanism (85% of the total). Thus, this movement is dependent on the water dynamics in the soil-plant system, driven by the plant transpiration [13].

Therefore, the process of absorption is the entry of an element, generally in ionic form, into any part of the cell or plant tissue [7].

The absorption process (passive and active) of magnesium in the form of Mg^{2+} , is much studied, since high concentrations of Ca^{2+} , and mainly K^+ in the medium, can inhibit the absorption by ionic competition, possibly causing deficiency in the plants. The rate of magnesium absorption can be affected by other cations such as K^+ , NH₄, Ca²⁺ and Mn^{2+} , as well as H⁺ under low pH conditions. Mg deficiency induced by the presence of another cation has been frequently observed [10].

After absorption, Ma^{2+} is transported from the roots to the aerial part through the interior of the plant, giving this process the name of translocation [14]. This step takes place through the xylem via the transpiration stream, basically in the way it was initially absorbed (Mg²⁺).

3.2 Redistribution

Redistribution is the transfer of an element from one organ or region of accumulation to any other. For example, ions stored in leaves during growth stages can be displaced prior to the onset of senescence and abscission, thus being redistributed to other organs, e.g. younger leaves, reserve organs, fruits and/or growth regions [7].

This redistribution (remobilization) of elements differs between nutrients and is reflected in the location of visual symptoms of nutritional deficiency in plants. Deficiency symptoms in older leaves correspond to a high rate of nutrient remobilization, while in younger leaves and apical meristems reflect insufficient redistribution. The redistribution occurs predominantly by the phloem [13].

Contrary to what occurs with $Ca²⁺$ and, similarly to what happens with K^+ , Mg²⁺ is mobile in the phloem and, as most of the plant's Mg is found in the soluble form, this explains its rapid redistribution in plants [7].

4. PARTICIPATION OF MAGNESIUM (Mg2+) IN PLANT METABOLISM

In plant tissues a high proportion of the total Mg about 70% is found in the diffusible form and associated with inorganic and organic anions such as malate and citrate. It is also associated with indifusible anions such as oxalate and pectate. [15].

The functions of magnesium in plants are mainly related to its ability to interact with nucleophilic ligands, for example, phosphoryl groups, through ionic bonds, and acting as a binding element and, or, forming complexes of different stabilities. Although many of the bonds involving magnesium are mainly ionic, some are covalent, as in the chlorophyll molecule [16]. Magnesium forms ternary complexes with enzymes in which binding cations are needed to establish a precise geometry between enzyme and substrate, as occurs in RuBPcarboxylase. A large proportion of the plant's total magnesium is involved in regulating cellular pH and cation-anion balance.

As a way to solidify what was previously presented, plants absorb magnesium as the Mg^{2+} cation and, once inside the plant, it performs several functions. Magnesium is the central atom of the chlorophyll molecule, thus it is actively involved in photosynthesis. Moreover, along with nitrogen they are the only soil nutrients that are constituents of chlorophyll. Most of the magnesium in plants is found in chlorophyll [17].

The functions of magnesium in plant metabolism are [9]:

Chlorophylls: are magnesium porphyrins, whose molecular weight contains 2.7% Mg. It represents about 10% of the total leaf Mg content. Plastids, however, have more magnesium than is contained in chlorophyll. Energy conversion is one of the main functions of chloroplasts, and Mg activates enzymes related to energy metabolism [18].

Chlorophylls are located in chloroplasts, this organelle being the continent of photosynthesis, that is, where the two important reactions take place: the photochemical one, in the thylakoid membranes, and the biochemical one, in the chloroplast stroma [19]. Chlorophylls have a porphyrin-like ring structure with a coordinated magnesium (Mg) ion at the center and a long tail of hydrophobic hydrocarbons that anchor them to photosynthetic membranes. The porphyrin-like ring is the site of electronic rearrangements that occur when chlorophyll is excited and of unpaired electrons when it is oxidized or reduced. The various chlorophylls differ mainly in the substituents around the rings and in the patterns of double bonds [20].

"**Phosphorus Charger":** it is found in the literature that Mg would be a phosphoruscarrying element, that is, it would contribute to the entry of P into the plant. The absorption of P (in the form of H_2PO^4) is maximum in the presence of Mg^{2+} , having the role of a "phosphorus carrier", probably due to its

participation in the activation of ATPases [3]. This effect is also believed to be due to the role of Mg in phosphorylation reactions. This role has a possible practical aspect: that of increasing the efficiency of phosphorus absorption by the roots.

The presence of other ions in the solution, such as magnesium, has a synergistic effect on phosphorus absorption, considering that Mg works as a P carrier. Thus, in an experiment with barley, it was observed that the presence of Mg together with "Marked" P, increased P absorption from the root and transport to the shoot.

Enzyme activation: Mg activates more enzymes than any other element. A fundamental role of this element is to be a cofactor of almost all phosphorylative enzymes, forming a bridge between ATP or ADP pyrophosphate and the enzyme molecule that act in reactions of synthesis of organic compounds (carbohydrates, lipids and proteins), ionic absorption and root expansion [21].

The transfer of energy from these two compounds is fundamental in the processes of photosynthesis, respiration, synthesis reactions of organic compounds, ionic absorption and mechanical work performed by the plant.

The lack of Mg inhibits $CO₂$ fixation even if chlorophyll is present: the element is required in phosphorylation reactions as well as in other phosphorylation reactions that limit the regeneration of ribulose diphosphate – the sugar that receives photosynthetically fixed carbon dioxide. Furthermore, it is required for the activity of the very enzyme that does this, namely ribulose diphosphate carboxylase.

Nitrogen metabolism is also influenced: in plants deficient in Mg, the protein N content is lower, increasing the non-protein N content, which shows that the lack of magnesium affects protein synthesis; the activation of the amino acids, an obligatory preliminary in the process, requires Mg; the transfer of activated amino acids to form the polypeptide chain or protein requires magnesium.

5. NUTRITIONAL REQUIREMENTS OF CROPS

The total Mg content in the plant can range from 1.5-3.5 g $kg⁻¹$. These values may vary depending on culture and other factors. Therefore, for a proper discussion of the nutritional requirement of crops, two factors are equally important: the total extraction/export of the nutrient, and the rate of absorption of this nutrient throughout the crop.

5.1 Nutrient Extraction and Export

The extraction or absorption of nutrients refers to the amount of a given nutrient that the plant needs to remove from the soil and/or the air to produce a ton of product, in the case of soybeans it is for a ton of grains. This extracted nutrient value expresses the amount of nutrient that is exported by the harvested product and the amount that remains in the plant remains after harvesting. While the export of nutrients from a crop refers to the amount of macro and micronutrients effectively removed by the grains or dry mass produced. In the case of soybeans, normally the export of nutrients is expressed in kg Mg⁻¹ of grains, since the product removed from the crop is the grains [22].

The crops that most extracted Mg per area were sugarcane and corn, 52 and 48 kg ha^{-1} , respectively, while wheat and rice extracted only 9 kg ha $^{-1}$.

Common bean exported the most Mg through grains (5.0 kg t^{-1}). Thus, it is important to monitor this crop for periodic replacement of this nutrient via corrective material (dolomitic limestone), since it is the lowest cost source of Mg.

Among annual crops, considering the need for Mg per ton of grain produced, legumes (8.7 to 18.5 kg t^{-1}) were more demanding than grasses $(3$ to 7.5 kg t⁻¹). Regarding the export of nutrients by grains produced by annual crops, it is noted that legumes (2 to 5 kg t^{-1}) export more than grasses (1.3 to 2.0 kg t^{-1}).

5.2 Nutrient Absorption Rate

Up to 59 days (12th leaf), the absorption of Mg by maize was considered slow, reaching only 16% of the total and, from this period on, the absorption was accelerated with peaks of high absorption speed between the 12th leaf and tanning and in the milky grain phase and "tooth" formation.

6. EFFECT OF MAGNESIUM ON ALUMINUM TOXIDITY ATTENUATION

At micromolar concentrations, Al causes rapid inhibition of root elongation in many species, which ultimately results in decreased water and nutrient uptake by plants. Many plants are able to resist or tolerate the harmful effects of Al stress better than others. The resistance mechanism now reported in a wide variety of plant species depends on the efflux of organic anions (malate, citrate and oxalate) from the roots [23].

Alleviation of Al toxicity by cations has been reported many times. In general, the effectiveness with which cations relieve Al stress depends on their concentration and valence, with trivalent cations being more effective than divalent cations, which are more effective than cation monovalent [24].

A series of detailed studies have demonstrated that several factors may be contributing to this response, including changes in the ionic strength of the solution and changes in the surface charge density of root cell membranes that affect the electrostatic interaction between free ions and the membrane surfaces [24]. One cation that has been shown to interact with Al toxicity in several different ways is the essential macronutrient magnesium (Mg).

Mg2+ binds relatively weakly to negatively charged groups in the root cell wall, so other cations, such as H^+ and Al^{3+} , present in acidic soils can impair Mg^{2+} loading in the apoplast and inhibit its uptake.

 Al^{3+} and Mg^{2+} ions compete for membrane transporters and metal binding sites on enzymes [25]. Both Al^{3+} and Mg²⁺ ions are hexahydrated, with the hydrated radii of Al^{3+} (0.480 nm) and Mg^{2+} (0.428 nm) being remarkably similar; therefore, the Mg²⁺ uptake system or the Mg²⁺ binding sites on enzymes do not distinguish well between Al^{3+} and Mg^{2+} ions.

The sites of toxic action of Al^{3+} on Mg absorption and homeostasis are competition for binding sites in the apoplast, inhibition of the activity of Mg^{2+} transporters and Mg^{2+} permeable cation channels, competition between Mg^{2+} and Al^{3+} for sites on enzymes, ATP and other molecules within the cell. Thus, good Mg nutrition can inhibit, at least in part, the toxic action of $Al³⁺$ [26].

7. SOURCES OF MAGNESIUM

Dolomitic limestone is commonly used as the main source of magnesium, as it not only corrects the pH but also provides calcium and magnesium.

Other mineral sources of Mg consist mainly of sulphates, Mg oxides, basic slag, potassium and magnesium sulphate and thermophosphates. In Brazil, calcined limestones composed of Ca (26 to 32%) and Mg (9 to 15%) are still widely sold, being one of the excellent sources of this nutrient.

The use of these sources varies according to nutrient content (Mg and other elements) and solubility, which controls nutrient availability to plants. These two factors determine the use of different mg sources in agricultural and horticultural systems.

The forms of magnesium sulfate are highly soluble compared to limestone, being the most used source in soils that need a quick response to this nutrient, while carbonates and oxides are poorly soluble forms in water and need to react with acids to release the magnesium. The supply of Mg through the application of lime must be carried out when the soil presents acidic conditions, otherwise it is recommended to use soluble salts or other sources of Mg [7].

8. SYMPTOMATOLOGY OF NUTRI-TIONAL DEFICIENCIES AND EXCESSES

Visual diagnosis is an important tool to assess the symptoms of deficiency or toxicity of an element by the appearance of the plant, especially by the color of its leaves [27].

8.1 Mg Deficiency

Soil Mg deficiency can arise under the following conditions:

- Acidic soil (pH <5.4);
- CTC Mg proportion less than 6%;
- High K content;
- Ratio K/Mg>4 e;
- Content less than 48 mg $dm³$ or 0.5 cmolc dm³ of Mg²⁺ in the soil.
- Soils derived from Mg-poor rocks;
- Light soils with little organic matter;
- High K:Mg ratio

As most of the Mg in the plant is found in the diffusible form and the element is mobile in the phloem, deficiency symptoms occur in older leaves. These manifest as an interveinal chlorosis, ie the deficiency appears as a yellowish, tan or reddish color while the leaf

veins remain green (coarse reticulate). In addition, there is a reduction in production and with the fall of leaves, the alternation of crops in perennial plants is accentuated [28].

In the case of maize, the leaves have yellow stripes and green veins. In general, it is noted that interveinal chlorosis is accompanied by yellowish spots that can unite forming bands along the margins of the leaf, which become reddish or other pigmentation. It should also be noted that chlorosis starts with spots that later join and spread to the tips and margins of the leaves.

However, the symptoms of Mg deficiency may vary depending on the species and/or cultivar. In leaves, mesophyll cells close to the vascular bundles retain chlorophyll for a longer period than parenchyma cells, which may delay the appearance of chlorosis.

Accumulation of non-structural carbohydrates (starch, sugars) is typically a characteristic of Mg^{2+} deficient plants. Thus, in common bean, the accumulation of carbohydrates in the leaves is related to the decrease in carbohydrate content in the drain regions, as occurs in roots and pods. Plants deficient in Mg often show a delay in the reproductive phase [29].

Accumulation of non-structural carbohydrates (starch, sugars) is typically a characteristic of $Mg²⁺$ deficient plants. Thus, in common bean, the accumulation of carbohydrates in the leaves is related to the decrease in the carbohydrate content in the drain regions, as occurs in the roots and pods.

In Mg deficiency, there is less translocation of carbohydrates from the aerial part to the root, impairing the development of the root system, which in turn will reduce the absorption of other nutrients.

8.2 K, Ca, Mg Interactions

The increase in K doses causes a decrease in Ca and Mg contents which, in extreme doses, can cause a drop in production. In this sense, foliar contents close to 1.8% of K provide an acceptable decrease in foliar Ca and Mg with satisfactory production. However, higher levels of K lead to a very sharp drop in the contents of Ca and Mg in the leaves, in a way that should be avoided in the management of potassium fertilization.

It is added that the preferential absorption of K is due to the fact that it is a monovalent ion with a lower degree of hydration compared to the divalent ones.

When the Ca/Mg ratio becomes too high, the plant can absorb less magnesium. This occurs when using only low-Mg limestone for a long period of time in relatively magnesium-poor soils. Mg deficiency induced by excess K in fertilization is quite common in crops such as banana and coffee (very demanding in K) where the formulas used are very rich in potassium. In acid soils, in addition to the natural poverty of Mg, the absorption of the element is reduced by H^+ and Al^{3+} , which appear in higher concentrations under these conditions.

8.3 MG X MN/ZN Interactions

The absorption of manganese and zinc can be affected by the higher concentration of magnesium, since they are elements with similar valence, ionic radius and degree of hydration [30].

In an experiment on the influence of magnesium on the absorption of manganese and zinc by detached soybean roots, it was observed that the increase in Mg doses decreased the absorption of Mn and Zn, by non-competitive inhibition [31].

8.4 Excess/Toxicity

The supply of magnesium at excessive levels results in the deposition of the element in the form of different salts in cell vacuoles, and harmful effects on the development and production of plants are not described in the literature.

Excess of Mg can cause deficiency of K and mainly of Ca.

9. CONCLUSION

Magnesium plays a fundamental role in the growth and development of plants. Thus, it is important to know its participation in the soil-plant system, in all its "compartments" that the nutrient travels from the soil solution, root and area part, to its incorporation into an organic compound or as an enzymatic activator, playing a role vital functions to enable maximum accumulation of dry matter in the final agricultural product.

In short, it stands out for actively participating in a series of vital processes (structural function) in plant metabolism, mainly as a central and essential component of the chlorophyll molecule framed as the main function of this element, in addition to acting as an enzymatic activator.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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