METAL IONS IN BIOLOGICAL SYSTEMS

Edited by

Helmut Sigel
Institute of Inorganic Chemistry
University of Basel
CH-4056 Basel, Switzerland

and Astrid Sigel

VOLUME 26

Compendium on Magnesium and Its Role in Biology, Nutrition, and Physiology

MARCEL DEKKER, INC. New York and Basel

Copyright © 1990 by Marcel Dekker, Inc.

3

Magnesium in Plants: Uptake, Distribution, Function, and Utilization by Man and Animals

S. R. Wilkinson
Southern Piedmont Conservation Research Center, USDA-ARS
1420 Experiment Station Road, P. O. Box 555, Watkinsville,
GA 30677, USA, and

Ross M. Welch
North Atlantic Area U.S. Plant, Soil and Nutrition Laboratory,
USDA-ARS, Tower Road, Ithaca, NY 14853-0331, USA, and

H. F. Mayland
Snake River Conservation Research Center, USDA-ARS, Route 1,
Box 186, Kimberly, ID 83341, USA, and

D. L. Grunes
North Atlantic Area U.S. Plant, Soil and Nutrition Laboratory,
USDA-ARS, Tower Road, Ithaca, NY 14853-0331, USA

1. INTRODUCTION 34

2. SOILS AS A SOURCE OF Mg FOR PLANT UPTAKE 35

2.1. Distribution, Forms, and Concentrations in Soil 35
2.2. Soil Factors which Affect Mg Uptake 35

3. CLIMATIC FACTORS AFFECTING Mg CONCENTRATION 36

3.1. Seasonal Factors 36
3.2. Temperature 37
3.3. Light Intensity 37

4. MAGNESIUM FUNCTION, UPTAKE, AND UTILIZATION 37

4.1. Biochemical Function 37
4.2. Plant Mg Absorption and Translocation Mechanisms 41

4.3. Distribution of Mg within the Plant 44
4.4. Deficiency Symptoms 45
4.5. Critical Mg Concentrations 46
4.6. Genotypic Influence on Mg Concentration in the Plant 47

5. CROP RESPONSES AND MAGNESIUM FERTILIZERS 48

5.1. Crop and Forest Responses 48
5.2. Magnesium Fertilizers 50

6. PLANTS AS A SOURCE OF Mg FOR ANIMAL AND HUMAN NUTRITION AND HEALTH 50

6.1. Ruminants and Grass Tetany 50
6.2. Humans 51

7. SUMMARY 51

REFERENCES 52

1. INTRODUCTION

Plants provide man with his primary needs—nutrition, clothing, and shelter as well as medicinal, recreational, and esthestic benefits. There are over 500,000 species of plants distributed over the earth.

Magnesium is an essential nutrient for plants and animals. The criteria for the essentiality of elements for plants are as follows: (1) the plant will be unable to complete its life cycle if the element is removed from the plant nutrient medium; (2) the element has a specific function which cannot be replaced by other elements; or (3) the element is a necessary component of an essential metabolite [1]. The relative abundance of Mg in plant life is less than N, K, Ca, and similar to S and P. Intensive crop production practices with fertilizers, improved plant cultivars, and best management practices are commonly used today. These intense cultural practices may mean an increasing frequency of Mg deficiencies as well as the need for knowledge on economically sound practices to prevent such deficiencies.

Plants are an important source of Mg to satisfy human and animal requirements, and factors affecting Mg bioavailability need to be identified. The objective of this chapter is to assess the importance, distribution, function, and utilization of Mg in plant growth and metabolism and in grazing ruminant animal production and human health.

2. SOILS AS A SOURCE OF Mg FOR PLANT UPTAKE

2.1. Distribution, Forms, and Concentrations in Soil

Magnesium occurs in soils in basically three fractions: nonexchangeable, exchangeable, and water-soluble. Magnesium uptake by plants occurs as Mg^{2+} (soluble) from soil solution.

2.2. Soil Factors Which Affect Mg Uptake

2.2.1. Soil pH and Type

The availability of soil Mg is reduced by competition from H, Al, and Mn at acidic pH values. On alkaline soils, carbonate formation and excess Ca, K, and Na reduce Mg availability. Effects of H^+ concentrations per se are considered to be less significant than changes in the availability of competing cations.

Magnesium availability to plants is affected by the parent material, duration and intensity of weathering, and capacity of soil to retain and supply Mg. For example, Mg deficiencies are less likely on Alfisols than on Ultisols, and less likely on Mollisols than Alfisols. An important aspect of soil type is rate and amount of Mg released from nonexchangeable sources.

2.2.2. Supply and Proportion of Other Ions

Increasing Ca saturation of the cation exchange complex (CEC) reduces Mg concentration. An excess of gypsum in alkaline soils can cause Mg deficiency. Excess Ca usually reduces Mg concentration less than does K. The mechanism for Ca reducing Mg uptake is attributed to competition via mass action rather than to specific competitive effects.

High K concentrations can be found in plants grown on soils with low exchangeable K, but it is unlikely that low K concentrations will be found in plants growing on soils with high levels of exchangeable K. A low Mg concentration in crops is likely where soil-exchangeable Mg is low, but a high exchangeable Mg content does not guarantee a high Mg level in crops. The proportion of the three cations K, Ca, and Mg may vary widely before plant growth is greatly reduced [2]. A severe Mg deficiency in most crop plants is unlikely when the soil exchange capacity is saturated with at least 6% Mg [3]. The magnesium concentration in plants increases when percent Mg saturation in the soil increases [2].

Short-term interruption of K supply rapidly increased the uptake of Ca and Mg in *Triticum aestivum* [4] and in *Phaseolus vulgaris* L. [5]. The rate of Mg uptake doubled when K concentration at the

root surface in soil solution decreased below 20 µmol K/l. Magnesium uptake at the root surface was inhibited by K concentrations above 20 µmol K/l [6].

Crop fertilization with acid-forming N fertilizers (ammonium) increases soil acidity and enhances differential K, Ca, and Mg loss from the soil [3]. Increased soil acidity also increases H^+ and Al^{3+}, with the latter possibly competing with Mg^{2+} for absorption by the root or reaching toxic levels where plant injury occurs. The mobility of Mg in soil increased when the dominant anion was NO_3^- compared with Cl^-, SO_4^{2-} or PO_4^{3-} [7].

Ammonium can be antagonistic to Mg uptake by plants, while NO_3 fertilization often enhances Mg uptake [8]. An interaction can occur with NO_3 fertilization which may result in NO_3 stimulating K^+ uptake which in turn reduces net Mg^{2+} translocation to plant tops [9].

There is convincing evidence that Al in soluble form or in exchangeable form in the soil interferes with Ca and Mg uptake in *Triticum* [10], *Avena* [11], *Glycine* [12], *Zea mays* [13], *Dactylis glomerata* [14], and *Picea* [15]. Aluminum also reduces Mg uptake more than K and Ca. Root metabolism may also be affected, further decreasing the ability of the root to absorb Mg from soil solution. Lohnis [16] found that applications of $MgSO_4$ decreased the Mn toxicity in several plants while having no effect in some other crops. Increased levels of Mg in nutrient solution alleviated symptoms of Mn toxicity, decreased Mn concentration in shoot and root tissues, reduced Mn absorption, and increased the growth of *Cucumis melo L.* [17]. Hecht-Buchholtz et al. [15] found that increasing Mn concentrations in nutrient solution from 3 to 920 mM reduced K concentration by about 5%, Ca concentration by about 35%, and Mg concentration by about 72% in *Picea abies* seedlings. Increasing levels of soluble Mn in the soil solution also may reduce Mg absorption.

3. CLIMATIC FACTORS AFFECTING Mg CONCENTRATION

3.1. Seasonal Factors

Many reports indicate that Mg concentrations of perennial grasses are higher in summer and fall than in spring [18,19]. However this seasonal effect is due at least in part to variation in physiological age of tissue [20]. Greene et al. [21] observed that ratios of live/dead plant tissue in the sample may contribute to these seasonal differences. Concentrations of Mg and K averaged 1.3 and 20.2 g/kg in live warm season grass tissue and 0.9 and 5.7 g/kg in dead tissue, respectively. Magnesium concentrations increased in leaf blades of timothy and bromegrass with progressive stages of maturity [22]. Increases in Mg concentration over the season were greater than changes brought about by Mg fertilization [19,23]. In perennial cool season

grasses, higher levels of exchangeable soil Mg or fertilizer Mg were required to increase Mg levels in early spring growth than in summer growth [23].

3.2. Temperature

Plants grown at warmer temperatures usually have higher Mg concentrations than when grown at lower temperatures [24]. Changing temperatures from cool to warm increased concentrations of K, Ca, and Mg, with the greatest increase occurring in K, and in increasing K/(Ca + Mg) molar ratios [8]. Magnesium deficiency in tomatoes grown in rock wool was worse at lower temperatures [25]. Magnesium concentration in grasses from the Himalayan grasslands was negatively correlated with rainfall (−0.58) and temperature (−0.50) [26].

3.3. Light Intensity

Agropyron desertorum and *Psathyrostachys juncea* grasses had higher Mg, Ca, K, N, organic acids, and higher fatty acid concentrations and reduced concentrations of total water-soluble carbohydrates when grown under reduced light conditions in the field [8]. Barta and Tibbitts [27] grew lettuce in recirculating nutrient solution under a 16-hr day and found that Ca and Mg concentrations were lower during daylight hours because of increased dry matter, i.e., growth dilution. Concentrations of Ca and Mg increased during the night with respiration losses of dry matter. Seasonal and climatic factors as well as physiological maturity of plants and their rates of growth affect Mg concentration. Growth dilution also occurs when other growth-limiting factors are removed from the plant's environment [28].

4. MAGNESIUM FUNCTION, UPTAKE, AND UTILIZATION

4.1. Biochemical Function

The numerous biochemical roles that Mg plays in plant metabolism are discussed in several reviews [29–33]. Generally, Mg forms bonds with ligand groups of cell metabolites that contain highly polarized ligands [34], like an O atom in phosphate and carboxylate anions. Magnesium prefers binding to N over neutral O species because of the greater polarizability of N. Most monodentate ligands that bind metal ions in cells will prefer Mg over Ca ions. Neutral O species will select Ca^{2+} over Mg^{2+} ions because of their low polarizability and low electric field strength.

Coordination chemistry has been used to describe the ability of the Mg^{2+} ion to form multidentate ligand complexes with metabolites

[34]. Magnesium tends to form regular octahedrons [30]. Because of its small atomic radius and its tightly bound water of hydration, a Mg^{2+} ion usually binds to only one or two ligand centers when forming metal complexes, thus maintaining its regular octahedral structure with the remaining water of hydration. This property makes Mg^{2+} ions suitable for forming ternary complexes with enzymes which require a crosslinking cation in order to produce a desired geometry between the protein and the substrate before the reaction can proceed.

In summary, Mg performs biological functions under circumstances where there is a need for a small, strongly electropositive, mobile, divalent cation which will coordinate to strongly nucleophilic ligands primarily by ionic bonding without excessive geometric distortion. Many enzymes require this type of metal ion for activation; almost all enzymes that activate phosphorylation processes require Mg as a dissociable cofactor. This role of magnesium is discussed in greater detail in Chap. 7. Some specific processes in higher plants where Mg performs an essential function are discussed below.

4.1.1. Photosynthesis

The most well-known function of Mg in plants is its role as the central atom in the tetrapyrrole ring of both the chlorophyll a and chlorophyll b molecules within plant leaf chloroplasts. Magnesium must be incorporated into the chlorophyll molecule before chlorophyll is effective at gathering light for photosynthetic carbon reduction reactions [32,35,36]. Incorporation of the Mg atom into the chlorophyll molecule results in this molecule having the necessary structure to absorb the quantum of light energy required to drive photosynthetic reactions. Apparently, the Mg^0 atom and the Mg^+ ion, and not the Mg^{2+} ion, are involved in absorption of light energy in chlorophyll molecules [36]. Although chlorophyll serves as the primary absorbent of radiant solar energy, the mechanism by which it transfers that energy to photosynthetic reactions is still a matter of speculation.

In addition to the role of Mg in light absorption in the chlorophyll tetrapyrrole ring, it is also involved in CO_2 assimilation reactions in the chloroplast [35]. Both photophosphorylation and phosphorylation reactions that occur in the chloroplast are affected by Mg ions [32]. For example, Mg is involved in CO_2 fixation by modulating ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBP carboxylase) activity in the stroma of chloroplasts [31]. This enzyme's activity is highly dependent on pH and Mg concentration. When Mg binds to this enzyme, the affinity of the enzyme for CO_2 is increased (i.e., the K_m is lowered), its turnover rate (i.e., V_{max}) is increased, and there is a shift in the optimum pH for the reaction

to a pH near neutrality [31,37]. Light triggers the activation of RuBP carboxylase in chloroplasts via its effect on the movement of Mg^{2+} and H^+ ions between the stroma and thylakoid compartment (i.e., granum) of chloroplasts. This light-induced reaction raises the pH and doubles the concentration of Mg in the stroma (e.g., Mg increases from 2 to 4 mM in the stroma). The magnitude of change in Mg^{2+} and H^+ ion concentrations is enough to result in an increase in the activity of RuBP carboxylase and in other stromal enzymes which are dependent on Mg and have pH optima over 6.

Examples of other enzymes affecting sugar phosphate anabolism in chloroplasts that can use Mg as a dissociable activator include fructose-1,6-bisphosphatase (FBPase) and glutamate synthetase. Changes in stromal pH and stromal Mg concentration in chloroplasts affect the activity of FBPase [38]; FBPase activity regulates the partitioning of assimilates between triose phosphate export from the chloroplasts and starch synthesis within the chloroplasts. Nitrate reductase is found in cytosols but nitrite reductase is confined to plastids [39]. Glutamine synthetase is found both in the cytosol and in the chloroplast. Thus, Mg plays a role in the reduction of nitrite in the chloroplast to ammonia and the incorporation of ammonia into glutamic acid via its function as an activator of glutamine synthetase [31].

4.1.2. Protein Synthesis

A large proportion (i.e., 75% [29]) of the Mg in leaf cells is associated either directly or indirectly with protein synthesis via its roles in ribosomal structure and function [31]. Magnesium is required for the stability of ribosomal particles, especially the polysomes; functional RNA protein particles require Mg to perform the sequential reactions needed for protein synthesis from amino acids and other metabolic constituents. The assemblage of ribosomal subparticles is partially controlled by Mg. Ribosomal subunits are unstable at Mg^{2+} concentrations less then 10 mM. They dissociate into smaller inactive particles unless at least this critical Mg ion concentration is maintained.

Important components of the protein-synthesizing system in plant cells that require Mg include both amino acid activation, polypeptide chain initiation, and polypeptide chain elongation reactions [40]. Also, Mg is required for RNA polymerase activity and thus for the formation of RNA in the nucleus [31]. The principal sites of Mg binding to RNA are the phosphate groups of RNA. Furthermore, Mg may bind the transfer aminoacyl-tRNA complex to the ribosome during protein synthesis [29].

4.1.3. Energy Mediation

Mitochondria in plant cells undergo structural degeneration without adequate amounts of Mg [41]. This may occur because many respiratory enzymes, like phosphatases, ATPases, and carboxylases, in the mitochondria require Mg. Thus, Mg plays a central role in ATP and energy metabolism. Because Mg is preferentially bound to phosphoryl groups, it forms a Mg-ATP complex. This complex can be used by the active sites of ATPases for transferring energy-rich phosphoryl groups. Magnesium is absolutely required for the synthesis of ATP acting as a bridging constituent between the enzyme and ADP [31].

4.1.4. Lipid Metabolism

Besides being required for the activation of several enzymes involved in the anabolism and catabolism of lipids, e.g., acetic thiokinase and various phospholipid-synthesizing enzymes [42], Mg is also involved in the biosynthesis of phospholipids and, therefore, in the formation of functional cell membranes [36].

4.1.5. Carbohydrate Metabolism

Nearly all phosphorylating enzymes involved in carbohydrate metabolism require Mg for maximum activity (e.g., UDP-D-, ADP-D-, and GDP-D-glucose pyrophosphorylase, and UDP-D-glucuronic acid pyrophosphorylase [43]). Many of these reactions require Mg because it can form complexes with phosphate groups. For example, during UDP-D-glucose synthesis via UDP-D-glucose pyrophosphorylase, $Mg(UTP)^{2-}$ and $Mg(PP_i)^{2-}$ serve as this enzyme's substrates and the velocity of UDP-D-glucose synthesis is a function of the Mg concentration [43]. Magnesium may also play a role in activating some of these enzymes in addition to its role in binding the nucleoside phosphates (e.g., in activating UDP-D-glucuronic acid pyrophosphorylase). Magnesium also functions in various enzyme activities associated with the glycolytic cycle.

4.1.6. Microtubule Assembly

Microtubules are one of three filamentous networks that form the cytoskeleton within eukaryote cells (actomyosin and intermediate filaments are the other classes of elements). They are cylindrical, hollow tubes of variable length composed of protein walls [44]. The tube wall protein is composed of 13 linear subunit strands (protofilaments). The protofilaments are made up of dumbbell-shaped subunits 4–5 nm in diameter that are heterodimers of α- and β-tubulin (a globular protein). The binding of Mg^{2+} to tubulin is required before tubulin polymerization occurs and microtubules assemble. It

is also required for the binding of GTP to the tubulin dimer. Thus, Mg is essential for the formation of microtubules in plant cells. Usually, 3–6 mM Mg is necessary to induce microtubule protein assembly in vitro.

4.2. Plant Mg Absorption and Translocation Mechanisms

The absorption by and movement of Mg within plants has not been studied very extensively. In order to understand Mg absorption and translocation, it is necessary to understand the absorption and translocation of K and Ca because these particular nutrients can have very large effects on Mg uptake and translocation. Potassium has been most intensely studied. Numerous mechanisms have been proposed to explain K uptake and translocation. However, even for K, considerable uncertainty exists as to the actual basic processes involved and how they are controlled. Here, we briefly discuss the most commonly accepted theories of K, Ca, and Mg absorption and translocation [31,45–48].

At soil solution K concentrations of 1 mM or less, the initial uptake of K across the outer cytoplasmic membrane of root cells bordering the root cell wall "free space" (i.e., epidermal and cortical cell plasmalemmas) is thought to occur via binding to a high-affinity carrier protein. This K-protein-carrier complex is thought to be transported across the plasmalemma. At the cell's interior, K^+ is released from the complex and the ion-free carrier protein is liberated to recirculate to the outer surface of the plasmalemma [46]. At soil solution concentrations of less then 1 mM, K absorption occurs against an electrochemical potential gradient. Thus, metabolic energy is consumed during K absorption by plant cells.

A second lower affinity, root cell, K transport system comes into play at higher K^+ concentrations in soil solution, (i.e., >1 mM). Possibly this mechanism is an ion channel extending across the root cell plasmalemma [46]. This system has a relatively low affinity for K ions and does not appear to be against an electrochemical potential gradient.

The high-affinity carrier protein (referred to as Mechanism I [1]) has a high selectivity and specificity for K^+; even relatively high concentrations of various monovalent cations, such as Na^+ or Li^+, or divalent cations, such as Ca^{2+} and Mg^{2+}, do not compare effectively for K absorption in this concentration range. Furthermore, accompanying anions (i.e., Cl^-, SO_4^{2-}) do not affect its activity. In comparison, the low-affinity, ion channel system (i.e., Mechanism II [1]) has a relatively low selectivity and sensitivity for K^+; various cations effectively compete with K^+ for uptake via this system including Na^+ and Ca^{2+}. Moreover, the type of anion markedly

affects K^+ uptake by this system. For example, SO_4^{2-} is much more effective than Cl^- in severely inhibiting K transport via Mechanism II. Both Mechanisms I and II operate simultaneously, but kinetically only Mechanism I is significant at soil solution concentrations of less then 1 mM.

Calcium and Mg absorption by plant cells have been investigated much less extensively than K absorption. However, interest in Ca has been stimulated because of the discovery of the Ca messenger system in plants [48]. The absorption of Ca is thought to be a "passive" process in which Ca is pumped inward by the large negative electrical potential that exists at the exterior surface of the plasmalemma [48–51]. The transient uptake of Ca into the cytoplasm is the result of an increased permeability of the cell membranes to Ca^{2+} ions. Cell membrane electrical potential fluctuations can open "channels" or "pores" specific for Ca ions. These allow Ca to move passively down its electrochemical potential gradient into the cytoplasm from the apoplasm. Certain proteins which span the membrane lipid bilayer may form the channels. Membrane pores which form Ca channels may be opened or closed by changes in the plasmalemma electrical potential. Numerous factors can influence the regulation of Ca channel gates (e.g., environmental stimuli such as temperature, nutrient supply, etc.).

Free (unbound) Ca^{2+} ion concentration in the cytoplasm of cells is rigorously controlled at very low levels (e.g., between 0.1 to 1 μM Ca) by homeostatic mechanisms involving active Ca extrusion "pumps" (i.e., Ca efflux carriers). These pumps transport Ca out of the cytoplasm into the cell wall apoplasmic spaces or into intracellular organelles (e.g., vacuole, mitochondria, endoplasmic reticulum, plastids, etc.), and by Ca binding to various nonmembranous molecules containing Ca-binding ligand groups (e.g., certain proteins such as calmodulin, adenine nucleotides, inorganic phosphate, and organic acids such as citrate and oxalate). The active extrusion of Ca from the cytoplasm is dependent on energy generated from the hydrolysis of ATP via an enzyme (Ca ATPase); Ca efflux is stimulated by increases in cytoplasmic calmodulin levels [48].

Magnesium absorption by plant cells has not been studied as extensively as either K or Ca absorption, and there is considerable uncertainty concerning Mg absorption. In earlier studies, [35,45], Mg absorption was reported to be an "active" process consuming metabolic energy. At low K concentrations (i.e., <1 mM) the rate of Mg absorption followed enzyme kinetics (i.e., the Michaelis–Menten equation). Thus, Mg absorption was thought to be carrier-mediated. High- and low-affinity absorption systems were proposed for Mg transport [52,53]. Others, however, reported that Mg absorption was a passive process [54,55] having many characteristics in common with Ca absorption. Therefore, Mg and Ca may be initially absorbed into root cells by

similar mechanisms, i.e., "passive" flux through a channel and not a carrier. Macklon and Sim [55] reported that Mg influx was passive; an active efflux pump was proposed to control free Mg^{2+} ion activity in the cytoplasm. Stok et al. [56] reported that Mg uptake was mainly active but that there was a passive Mg absorption component which was accompanied by Ca efflux. Thus, there is no consensus concerning the basic mechanisms of Mg absorption by root cells and further studies are required for clarification.

Magnesium can interact with a number of other mineral nutrients (e.g., Ca^{2+}, K^+, NH_4^+, and NO_3^-). Under some circumstances increased K or Ca supply to plants results in reduced concentrations of Mg in tops [35,57]. The negative effects of K^+ ions on the accumulation of Mg cannot be understood using current theories of K and Mg absorption by root cells. Possibly, the negative effects of K on Mg concentration in plant shoots is the result of reduced net translocation of Mg from roots to shoots and not to decreased uptake of Mg by root cells. An understanding of the mechanisms of translocation and mobilization of these ions between roots and shoots is necessary to understand Mg and K interactions.

Unfortunately, the mechanisms of K, Ca, and Mg translocation are not fully understood [58]. Potassium is thought to be delivered to vascular elements in the root via the symplasmic continuum (that links the cytoplasm of one cell to another through the intercellular conduits, the plasmodesmata) after being accumulated by epidermal and cortical cells from the root cell wall apoplasmic space. The present consensus of opinion suggests that K is actively pumped out of xylem parenchyma cells and into adjoining xylem vessels before being translocated to the shoot by mass flow with water driven upward by the transpiration stream. Some researchers have suggested that Ca^{2+} and Mg^{2+} ions do not follow this route but that they may follow a completely apoplasmic route into xylem vessels without ever entering the symplasm of root cells. This later view seems untenable for several reasons. First, the levels of Ca and Mg in xylem sap can reach concentrations in excess of those in the substrate bathing root cells. Second, the endodermis forms a suberized barrier to ion movement, i.e., the Casparian strip, which prevents the mass flow or diffusion of ions into the apoplasm of stellar cells from the apoplasm of cortical cells. Third, if there were an apoplasmic pathway for ion movement into xylem vessels, what would prevent K or another mineral nutrient from also passing into xylem vessels via this route? But K does not follow this route. Therefore, this hypothetical apoplasmic pathway for Ca and Mg movement would appear to be incorrect, and Ca and Mg should follow a symplasmic route into the stele where they are pumped into xylem vessels from xylem parenchyma cells before being translocated to the shoot.

How, then, does K inhibit net Mg movement to shoots from roots? It is unlikely that K would directly compete for Mg absorption sites at cell membrane surfaces because these ions are too dissimilar. Possibly the inhibition is the result of the stimulation of Mg recirculation from shoots to roots via the phloem as a result of increases in K supply. This suggestion is supported by the observation that high K treatments decrease Mg concentrations in leaves but enhance Mg movement into fruits and storage organs [45], and that the phloem, not the xylem, is known to be the principal conduit for the movement of mineral nutrients into these organs [58]. Furthermore, Mg mobility in *Lupinus albus* L. was reported to resemble K in showing substantial phloem transport and recirculation from the shoot to the roots [59]. Possibly K stimulates the loading of Mg into the phloem sieve tube elements in the shoot. This speculation awaits further research.

4.3. Distribution of Mg within the Plant

The concentration of Mg in plant organs and tissues not only varies among different plant species and varieties but also is influenced by the plant's stage of development (i.e., plant age). The Mg concentration is also affected by several environmental factors including the supply of mineral nutrients (e.g., K, Ca, and forms of N) and various meteorological factors [60,61]. Generally, legumes accumulate more Mg in their above-ground portions then do grasses. Angiosperms accumulate more Mg in their seeds than in their vegetative parts. Meristematic tissues and other rapidly metabolizing tissues also accumulate high Mg concentrations [33].

About 10% of the total Mg in mature leaves is bound to chlorophyll a and chlorophyll b [29]. Additionally, about 75% of the Mg in healthy plant tissues is associated with the structure and function of ribosomes. The remaining 15% is either free, ionic Mg^{2+} or Mg bound to various Mg-activated enzymes and to other cation binding sites associated with cells (e.g., various ligand groups of proteins, organic acids, and amino acids, and on cation exchange sites within the cell wall free space, i.e., within the apoplasm).

The water solubility of Mg in leaf tissue of various forage grasses and legumes was similar although minor differences did occur. Increasing N fertilization rates did not affect the proportion of water-soluble Mg in the plant [62]. Fertilization with Mg increased total Mg but did not greatly affect the proportion of Mg soluble in water, or in cells walls, or the chemical form [62,63].

The magnesium concentration in various plant parts is affected by Mg fertilization. Fertilization of sweet corn with 134 kg Mg/ha increased the yield of sweet corn 33%, Mg in sweet corn leaves 161%, and Mg in the grain 33%. Similar Mg treatments applied to snapbeans

did not increase the yield, but Mg concentration in leaves and petioles increased by 141%, while Mg in snapbean pods increased by 31% [64]. Grimme [65] found that Mg preferentially accumulated in grain when in low supply and accumulated in vegetative portions when in high supply. Reproductive structures have first priority on Mg supplies. When Mg supplies approach adequacy, vegetative structures then become storage sinks for Mg. Since Mg is mobile in the phloem, it can be recirculated to other organs.

4.4. Deficiency Symptoms

Symptoms of Mg deficiency differ among plant species and with the severity of the deficiency [29,60,66,67]. However, there are some general characteristics of Mg deficiency which are common to most higher plants. Loss of chlorophyll (chlorosis) in leaves is usually the first symptom of Mg deficiency manifested in higher plants. Because Mg is a phloem-mobile nutrient, chlorosis begins in the older leaves and progresses to younger leaves. In dicots chlorosis, which is generally interveinal, occurs within a persistent green leaf margin. In some dicots, the green margin can become yellow or brilliant orange-red or purple. The appearance of these colors can be spread over wide areas of the leaf or be confined to mottled areas between leaf veins. In some monocots, the base of the leaf initially develops dark green spots where chlorophyll has accumulated against a pale yellow background. With time the leaf becomes more chlorotic and striped. Necrosis generally starts at the leaf tip in monocots.

At the cellular level, Mg deficiency can result in granular inclusions in mitochondria. Additionally, large starch grains accumulate in chloroplasts and grana may be vacuolated and less numerous. In some species (e.g., *Zea mays*), chloroplasts lose their outer membranes and their contents spill into the cytoplasm and osmiophilic granules accumulate.

Other, less overt effects of Mg deficiency, besides yield reduction, are the following: increased evolution of ethylene [68,69], increased suberization of hypodermal and endodermal root cell walls [70], reduced frost hardiness in *Picea abies* [71], decreased assimilation of NH_4-N and NO_3-N in *Triticum aestivum* [72], retarded sucrose formation and pronounced starch accumulation in trifoliate leaves of *Phaseolus vulgaris* [73], reduced quality of *Solanum tuberosum* tubers [74], and reduced photosynthetic rates in *Populus euramerican* [75].

Magnesium also appears to ameliorate Ni toxicity [76] and Al toxicity by protecting root meristems [77]. Higher than normal levels of Mg have also been reported to protect against toxic levels of B [78]. In general, Mg appears to provide a protective function similar to that of Ca in maintaining plant tissue integrity and providing protection against adverse environmental conditions.

4.5. Critical Mg Concentrations

The critical Mg concentration is that value in a specified plant part where a previously specified reduction in yield occurs (usually 10%). It is determined from the relationship between yield and nutrient concentration depicted in Fig. 1.

The critical concentration of Mg for higher plant growth varies between plant species, plant part, and stage of development [29,32, 60,66]. Usually, plants whose leaves contain less then 0.2% Mg (dry weight) are considered to be Mg-deficient. Critical Mg concentrations are generally lower for monocotyledonous than dicotyledenous plants. Generally, leaves from plants containing more then 0.4% Mg (dry weight) are deemed adequate in Mg. Embleton [60] stressed that "when using tissue analysis in diagnosing magnesium deficiency, it is important to know the specific tissue sampled, the age, position on the plant, and whether or not symptoms of deficiency exist on the plant and on the tissue sampled". Table 1 lists some Mg concentration ranges reported for various plant species. Plucknett and Sprague [79] present mineral requirements for 46 crops. Magnesium toxicity is practically unknown. When growth reduction occurs, it usually is a result of an induced deficiency or toxicity of another element.

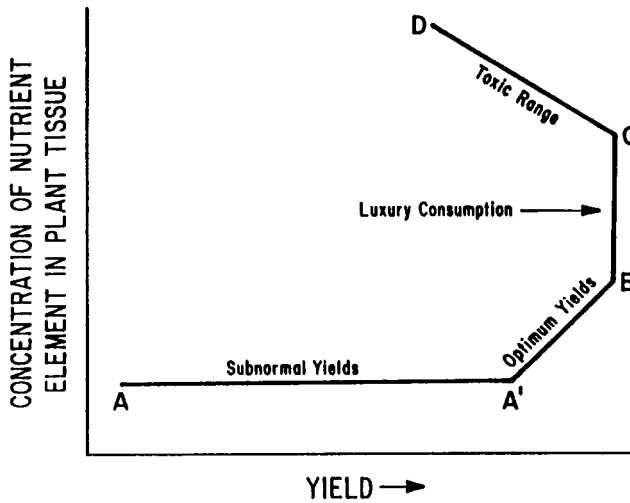

FIG. 1. Relationship of concentration of nutrient elements in plant tissue to yield. (From Beeson [98] by permission.)

TABLE 1

Magnesium Concentration Ranges in Representative Plant Species (% dry weight)

Species	Part	Deficient	Adequate
Citrus spp.	Leaf	<0.15	0.30–0.70
Beta vulgaris L.	Petiole	0.01–0.03	0.10–0.70
Beta vulgaris L.	Blade	0.025–0.05	0.10–2.50
Zea mays L.	Blade	0.07	>0.20
Brassica oleracea L.	Top	0.43	0.56–0.57
Cucumis sativus L.	New leaf	<0.35	0.5–0.9
Lactuca sativa L.	Head	0.05–0.10	0.24–0.48
Lycopersicon esculentum Mill	Leaf	0.12–0.19	0.40–0.60
Cynodon dactylon L.	Tops	0.10	0.15–0.60
Festuca arundinacea Schreb.	Tops	0.08	0.15–0.60
Medicago sativa	Tops	0.30	0.30–0.70
Stylosanthes	Tops	0.27	>0.30
Acer	Leaf	0.03–0.09	>0.09

Source: From Bould et al. [29]; Embleton [60]; Mengel and Kirkby [32]; Plucknett and Sprague [79]; Scaife and Turner [66]; Winsor and Adams [67]; Wilkinson and Mays [94]; Wilkinson et al. [95].

4.6. Genotypic Influence on Mg Concentration in the Plant

Differences in Mg concentration and nutrition associated with cultivars have been found in many species as well as between species. A comprehensive discussion of genetic factors which could potentially affect the ability of plants to absorb Mg is given by Gerloff and Gabelman [80]. Grass tetany may occur when a ruminant animal's diet contains insufficient available Mg. This economic problem has promoted plant-breeding research to increase Mg concentration in forage grasses and to increase its bioavailability. Genetic variation in Mg concentration in herbage has been measured in some C_3 grasses [81], and there is evidence that a breeding and selection program could increase the bioavailability of Mg. Selecting for higher Mg

concentrations in Italian ryegrass increased the Mg concentration and increased the bioavailability of Mg to sheep [82]. In addition, sheep ate more of the high-Mg selection.

5. CROP RESPONSES AND MAGNESIUM FERTILIZERS

5.1. Crop and Forest Responses

Magnesium deficiencies that affect forage dry matter production are not common since critical Mg concentrations are low (0.10%) for most plants (Table 1), and Mg removal from soils in harvested livestock products is low (Table 2). Most Mg deficiencies are induced by high levels of K or Ca, or by Al or Mn in acid soils. Shallow soils and coarse-textured soils may also result in crop Mg deficiencies. There is notable concern over the need to produce grass containing 2.5 g Mg/kg, the concentration thought necessary to prevent grass tetany in grazing, lactating ruminants.

Magnesium deficiency in small grains may appear in early season but not affect grain yields. This is attributed to the movement of Mg during senescence from older leaves to the developing grain. Magnesium is mobile within the plant, and the Mg in the flag leaf and recently matured leaves is important for grain production. This probably accounts for the dramatic effects of Mg deficiency in producing chlorotic leaves while yields of reproductive tissues may be decreased very little, if at all. Magnesium concentration in grain when compared with that in vegetative tissue is much less affected by low available soil Mg. Fertilization to increase Mg concentrations in grains is less efficient than in vegetative tissue [61]. Magnesium concentration in oily seeds is about 2.5 times greater than Mg in starchy seeds [83]. Magnesium removal in comparable dry matter yields of wheat grain are about one-half the Mg removal in soybean grain (Table 2). Nutrient removal is the product of concentration by crop yield. Yield is normally the primary factor in Mg removal.

Magnesium deficiencies appear more common in horticultural crops than in forage or grain crops. These deficiencies most often occur on sandy soils, in wet seasons, and in situations of high K-fertilizer usage. Sandy soils are often used extensively in horticultural crop production. Sensitivity to Mg deficiency varies among similar crops [66]. The amounts of Mg removed with the harvested crop range from relatively low amounts as in the case of *Triticum aestivum* to large amounts in the case of *Elaeis guincensis* (Table 2).

Magnesium deficiencies (and Ca deficiencies) have been reported in *Acer saccharum* [84], *Pinus sylvestris* [71], and *Picea abies* [15]. Abrahamsen [85] speculated that problems of Mg deficiency may be stimulated by acid precipitation where soil Mg is low or where Mg deficiency is incipient. Roy et al. [86] associated the decline of

TABLE 2

Magnesium Removal in Harvests of Various Crops

Crop name	Yield level (mg/ha)	Mg removal (kg/ha)
Triticum aestivum, grain	2.2	2
Triticum aestivum, straw	3.4	3
Zea mays, grain	9.5	9
Zea mays, straw	11	22
Medicago sativa L.	9	24
Cynodon dactylon L.	18	27
Festuca arundinacea shreb	8	20
Beta saccharifera	34	27
Saccharum officinarum	67	27
Solanum tuberosum	27	7
Brassica oleracea capitate	50	9
Elaeis guincensis (oil)	2.5	38
Glycine, grain	2.2	4
Citrus (orange)	63	13
Nicotiana tabacum leaves	2.2	16
Whole tree harvests[a]		2–9

[a]Amount removed for various forest ecosystems per rotation which varied in age from 30 to 150 years [97]. Actual amounts removed will vary with soil type, year, and soil fertility for each crop represented.
Source: Ref. 96.

A. saccharum in Quebec, Canada with appreciable deficiencies of soil Ca and Mg. *Picea abies* trees on podzol, podzolic cambisols, and eutrophic cambisols were Mg-deficient [87]. Increased and/or continued deposition of nitric and sulfuric acids stimulates problems of Mg deficiency and nitrogen imbalance. Continued forest health and production in some of these regions may require soil amendments containing Mg and Ca to improve tree growth, health, and vigor.

5.2. Magnesium Fertilizers

The effectiveness of Mg fertilizers is determined primarily by their particle size and water solubility. Fertilizers of varying immediate availability and residual value can be produced by manipulating particle size and water solubility. Soil application of Mg fertilizer is necessary when Mg deficiencies reduce economic yield or product quality. Surface placement of soluble Mg fertilizers is satisfactory, while soil incorporation is recommended for less soluble Mg sources. The effectiveness of surface applications of insoluble or slightly soluble materials depends on particle size. Foliar sprays made from soluble Mg salts ($MgSO_4$, $MgCl_2$, $Mg(NO_3)_2$, Mg chelate) can be effective in correcting crop Mg deficiency but must be repeated to maximize their effectiveness in preventing or correcting Mg deficiency. See Chap. 2 or [19] for a more detailed discussion of Mg fertilizers.

6. PLANTS AS A SOURCE OF Mg FOR ANIMAL AND HUMAN NUTRITION AND HEALTH

6.1. Ruminants and Grass Tetany

Grass tetany is a metabolic disorder of ruminants associated with low blood serum Mg levels. Grass tetany is a major health problem of cattle and sheep in temperate climates. The problem occurs most commonly when animals graze cool season grasses having C_3-type photosynthetic pathways. The etiology of the disorder is complex involving the soil-plant-animal-climate continum. Magnesium concentrations considered adequate to prevent tetany increase when forage K, N, organic acids, higher fatty acids, and water content increase. When available carbohydrates and dry matter intake increases, the "safe" concentration of Mg decreases.

The reader is referred to general reviews for more comprehensive coverage [88] and Chap. 4 of this volume. Mineral indices have been developed to characterize the grass tetany potential of the forage. The first of these is the K/(Ca + Mg) ratio, calculated on an equivalent basis. Equivalent ratios greater than 2.2 have been associated with forage prone to causing tetany in ruminant animals. This ratio accounts for the antagonism of forage K and benefits of forage Mg and Ca on Mg absorption by the animal [88]. Another index, known as the Dutch nomograph, described by Mayland and Grunes [8] uses Mg, K, and N concentrations in forage to predict dairy cow blood serum values and thereby indicate grass tetany hazard of the forage. Application of this nomograph to beef cows grazing *Festuca arundinacea* in northern Georgia was not successful [61]. However, the general principles illustrated by the nomograph were confirmed. Under conditions of limited Ca availability the K/(Ca + Mg) ratio may be more useful [88].

6.2. Humans

Primary Mg deficiency in humans is not widespread and is considered rare in people with normal organ function and reasonable diet selection and intake [89]. Magnesium deficiencies in humans are seen where special conditions exist, often of a pathological nature.

In normal diets, foodstuffs of plant origin provide about one-half the normal intake of Mg with animal products and supplements supplying the other half. Excellent plant sources of Mg are *Arachis hypogaea*, *Zea mays*, cereal grains, and leafy green vegetables. Foods of leafy origin contain relatively more Ca than Mg and those of grain origin less Ca than Mg. Prospects for increasing Mg concentrations by cultural practices are better in leafy vegetables than in fruits or seeds (grain).

The bioavailability of Mg in foods of plant origin has been investigated using stable ^{26}Mg (11.01% natural abundance) as a tracer. The usefulness of ^{26}Mg has been limited by its relatively high natural abundance. Recently, improved techniques such as secondary ion mass spectrometry [90] and inductively coupled argon plasma mass spectrometry [91] have improved the capability of elemental analysis and isotope ratio determinations. These developments should permit more sophisticated research using stable isotopes of Mg as tracers in plant and animal nutrition studies.

Schwartz et al. [92] grew leafy vegetables where ^{26}Mg replaced naturally occurring Mg isotope ratios. They found that the ^{26}Mg level in these crops was 87–92% of the total plant Mg. These leafy vegetables were later fed to human subjects [93], and values for the percentage of true absorption were calculated using ^{26}Mg determinations in plasma after intravenous and oral isotope administration. True absorption values were higher for leafy vegetables than for bran. Exchangeability of the extrinsic tracer (^{28}Mg) and the intrinsic tracer (^{26}Mg) was close to 100% in humans.

7. SUMMARY

Magnesium is essential for all life. Magnesium deficiencies in plants generally occur under severely weathered, wet, acid, or sandy soils, or where rooting volumes are restricted, but rarely where soil parent materials are inherently deficient in Mg. Most Mg deficiencies in cultivated crops occur as a result of excessive K fertilization, or high soil K levels. Recognition of the importance of Mg in nutrition of forest trees has increased recently because acid rainfall enhances leaching of Mg from soil and tree foliage. Reduced soil Mg available for root absorption is the result. The potential for grass tetany in grazing ruminants may also increase as a result of acid rainfall.

Magnesium is absorbed by plant roots from soil solution as Mg^{2+}, and is transported within the plant in both the apoplasm and the symplasm. Absorption from soil solution is affected by the quantity and proportions of competing cations (K, Ca, Al, and H). The net accumulation of Mg in plant tops may be decreased by high K concentrations in soil solution. The mechanism for this K antagonism is not known. Magnesium is normally mobile once absorbed by the plant. Magnesium accumulates in vegetative plant parts under conditions of high Mg supply, but concentrations of Mg in the seed are relatively constant whether the Mg supply is low or high.

The biochemical functions of Mg include its crucial role in light energy absorption in the chlorophyll tetrapyrrole ring, and in energy transfer, protein synthesis, lipid synthesis, and carbohydrate synthesis and translocation. Magnesium is a dissociable cofactor, or activator, for almost all enzymes that activate phosphorylation processes. Magnesium is essential for CO_2 fixation, and for chloroplast, mitochondria, and ribosome stability. The unique chemical properties of Mg enable plants to capture the sun's energy, convert it to stored energy, and enable this energy to be used to synthesize carbohydrate, lipid, protein, and other anabolic products.

REFERENCES

1. E. Epstein, "*Mineral Nutrition of Plants: Principles and Perspectives*", John Wiley and Sons, New York, 1972.
2. O. A. H. Johansson and J. M. Hahlin, in "*Proceedings International Seminar on Soil Environment and Fertility Management in Intensive Agriculture*", Tokyo, 1977, p. 487.
3. R. Ellis, Jr., in *Grass Tetany* (V. V. Rendig and D. L. Grunes, eds.), Special Publ. 35, Am. Soc. Agr., Madison, WI, 1979, pp. 79–92.
4. P. Jensen, *Physiol. Plant.*, *56*, 259 (1982).
5. A. Herman-McKentley, F. P. Gardner, and V. N. Schroder, *Proc. Soil Crop Sci. Soc. Fla.*, *41*, 139 (1982).
6. B. Seggewiss and A. Jungk, *Z. Pflanzenernähr. Bodenk.*, *151*, 91 (1988).
7. J. T. Gillingham and N. R. Page, *Agron. J.*, *57*, 83 (1965).
8. H. F. Mayland and D. L. Grunes, in *Grass Tetany* (V. V. Rendig and D. L. Grunes, eds.), ASA Special Publ. No. 35, ASA, Madison, WI, 1979, pp. 123–175.
9. J. Huang, D. L. Grunes, and R. M. Welch, *Agron. J.*, *82* (in press).
10. K. Ohki, *Agron. J.*, *77*, 951 (1985).
11. H. Grimme, *Z. Pflanzenernähr. Bodenk.*, *146*, 666 (1983).
12. H. Grimme, in Proceeding, "*VIth International Colloquium for Optimization of Plant Nutrition*", Vol. 1. Montpellier Cedex, France, 1984, pp. 243–249.

13. R. B. Clark, *Plant Soil, 47*, 653 (1977).
14. K. Kurashima and T. Kimura, *Bull. Nat'l. Grassl. Res. Inst., 36*, 28 (1986).
15. C. Hecht-Buchholtz, C. A. Jorns, and P. Keil, *J. Plant Nutr., 10*, 1103 (1987).
16. M. P. Lohnis, *Plant Soil, 12*, 339 (1960).
17. O. M. Elamin and G. E. Wilcox, *J. Am. Soc. Hort. Sci., 111*, 582 (1986).
18. J. R. Todd, *J. Agric. Sci.* (Cambr.), *57*, 35 (1961).
19. S. R. Wilkinson, in *Role of Magnesium in Animal Nutrition* (J. P. Fontenot, G. E. Bunce, K. E. Webb, Jr., Vivien G. Allen, eds.), Proceedings of John Lee Pratt International Symposium, John Lee Pratt Animal Nutrition Program, Virginia Polytechnic Institute and State U., Blacksburg, VA, 1983, pp. 61—80.
20. P. F. Reay and B. Marsh, *N.Z. J. Agri. Res., 19*, 469 (1976).
21. L. W. Greene, W. E. Pinchak, and R. K. Heitschmidt, *J. Range Manage., 40*, 502 (1987).
22. G. I. Pritchard, W. J. Pigden, and L. P. Folkins, *Can. J. Plant Sci., 44*, 318 (1964).
23. S. McIntosh, P. Crooks, and K. Simpson, *J. Agric. Sci.* (Camb.), *81*, 507 (1973).
24. D. L. Grunes and R. M. Welch, *J. Anim. Sci., 67* (in press).
25. C. Sonneveld, *J. Plant Nutr., 10*, 1591 (1987).
26. B. R. Singh and V. K. Mishra, *Soil Sci., 143*(4), 242 (1987).
27. J. Barta and T. W. Tibbitts, *Plant Physiol. (suppl.), 77*, 164 (1985).
28. J. J. Mortvedt and F. E. Khasawneh, *Soil Sci., 141*, 200 (1986).
29. C. E. Bould, E. J. Hewitt, and P. Needham, "*Diagnosis of Mineral Disorders in Plants, Vol. 1, Principles*", Chemical Publishing, New York, 1984.
30. D. T. Clarkson and J. B. Hanson, *Ann. Rev. Plant Physiol., 32*, 239 (1980).
31. H. Marschner, "*Mineral Nutrition of Higher Plants*", Academic Press, Orlando, 1986.
32. K. Mengel and E. A. Kirkby, "*Principles of Plant Nutrition*", International Potash Institute, Worblaufen-Bern, Switzerland, 1978.
33. J. R. Woodruff, in *Magnesium in the Environment, Soils, Crops, Animals, and Man* (J. B. Jones, M. C. Blount, and S. R. Wilkinson, eds.), Proceedings of a Symposium Held at Fort Valley State College, Fort Valley, Georgia, October 5—6, Taylor County Printing Company, Reynolds, GA, 1972, pp. 41-60.
34. P. K. Hepler and R. O. Wayne, *Ann. Rev. Plant Physiol., 36*, 397 (1985).

35. D. B. Hannaway, L. P. Bush, and J. E. Leggett, "*Plant Nutrition: Magnesium and Hypomagnesemia in Animals*", University of Kentucky, College of Agriculture, Agricultural Experiment Station Bulletin No. 716, Lexington, KY, 1980.
36. H. F. Mayland, in *Role of Magnesium in Animal Nutrition* (J. P. Fontenot, G. E. Bunce, K. E. Webb, and V. G. Allen, eds.), Proceedings of John Lee Pratt International Symposium on the Role of Magnesium in Animal Nutrition, John Lee Pratt Animal Nutrition Program Virginia Polytechnical Institute and State University, Blacksburg, VA, 1983, pp. 17-21.
37. M. F. Hipkins, in *Advanced Plant Physiology* (M. B. Wilkins, ed.), Pitman, London, 1984, pp. 219-248.
38. A. Gardemann, D. Schimkat, and H. W. Heldt, *Planta, 168*, 536 (1986).
39. T. A. P. Rees and D. D. Davies (eds.), in *The Biochemistry of Plants: A Comprehensive Treatise, Vol. 12, Physiology of Metabolism*, Academic Press, Orlando, 1987, pp. 87-115.
40. A. L. Lehninger, "*Biochemistry*", 2nd ed., Worth, New York, 1975.
41. N. G. Marinos, *Am. J. Bot., 50*, 998 (1963).
42. T. S. Moore, Jr., in *Current Topics in Plant Biochemistry and Physiology*, Vol. 3, Proceedings of the Third Annual Plant Biochemistry and Physiology Symposium, University of Missouri-Columbia, April 4–6, 1984, The Interdisciplinary Plant Biochemistry and Physiology Program, University of Missouri, Columbia, Missouri, 1984, pp. 100-107.
43. J. E. Gander, in *Plant Biochemistry* (J. Bonner and J. E. Varner, eds.), Academic Press, New York, 1976, pp. 337-380.
44. P. J. Dawson and C. W. Lloyd, in *The Biochemistry of Plants: A Comprehensive Treatise*, Vol. 12, "*Physiology of Metabolism*" (D. D. Davies, ed.), Academic Press, Orlando, 1987, pp. 3-47.
45. R. B. Clark, in *Soil Acidity and Liming*, 2nd ed. (F. Adams, ed.), Agronomy Monograph no. 12, ASA, Madison, WI, 1984, pp. 99-170.
46. L. V. Kochian and W. J. Lucas, *Adv. Bot. Res., 15*, 93 (1988).
47. U. Luttge, in *Inorganic Plant Nutrition* (A. Lauchli and R. L. Bieleski, eds.), Springer-Verlag, New York, 1983, pp. 181-211.
48. B. W. Poovaiah and A. S. N. Reddy, *CRC Crit. Rev. Plant Sci., 6*, 47 (1987).
49. D. T. Clarkson, "*Plant, Cell and Environment*", *7*, 449 (1984).
50. J. B. Hanson, *Adv. Plant Nutr., 1*, 149 (1984).
51. D. Marme, in *Inorganic Plant Nutrition* (A. Lauchli and R. L. Bieleski, eds.), Springer-Verlag, New York, 1983, pp. 599-625.
52. R. A. Joseph and T. Van Hai, *Physiol. Plant., 36*, 233 (1976).
53. E. V. Maas and G. Ogata, *Plant Physiol., 47*, 357 (1971).
54. N. Higinbotham, B. Etherton, and R. J. Foster, *Plant Physiol., 42*, 37 (1967).
55. A. E. S. Macklon and A. Sim, *Planta, 128*, 5 (1976).

56. B. P. Stok, O. G. Tanczos, M. Kahr, and C. E. E. (Bep) Stuiver, *Physiol. Plant.*, *52*, 115 (1981).
57. T. Ohno and D. L. Grunes, *Soil Sci. Soc. Am. J.*, *49*, 685 (1985).
58. R. M. Welch, *Adv. Plant Nutr.*, *2*, 205 (1986).
59. W. Dieter, J. S. Pate, and C. A. Atkins, *J. Plant Physiol.*, *128*, 77 (1987).
60. T. W. Embleton, in *Diagnostic Criteria for Plants and Soils* (H. D. Chapman, ed.), University of California, Division of Agricultural Sciences, Riverside, CA, 1966, pp. 225-263.
61. S. R. Wilkinson, J. A. Stuedemann, D. L. Grunes, and O. J. Devine, *Magnesium*, *6*, 74 (1987).
62. D. C. Whitehead, K. M. Goulden, and R. D. Hartley, *Anim. Feed Sci. Technol.*, *14*, 231 (1986).
63. J. R. Todd, *J. Agric. Sci.* (Cambr.), *58*, 277 (1962).
64. S. T. Than, Magnesium requirements for vegetable crops grown on certain Georgia soils. M. S. thesis. University of Georgia, 1955.
65. H. Grimme, *Landwirt. Forsch*, *40*, 356 (1987).
66. A. Scaife and M. Turner, "*Diagnosis of Mineral Disorders in Plants, Vol. 2, Vegetables*", Chemical Publishing, New York, 1984.
67. G. Winsor and P. Adams, "*Diagnosis of Mineral Disorders in Plants, Vol. 3, Glasshouse Crops*", Chemical Publishing, New York, 1987.
68. V. Barker and K. A. Corey, *Hortsci.*, *23*, 202 (1988).
69. T. Nur, R. Ben-Arie, S. Lurie, and A. Altman, *J. Plant Physiol.*, *125*, 47 (1986).
70. J. M. Pozuelo, K. E. Espelie, and P. E. Kolattukudy, *Plant Physiol.*, *74*, 256 (1984).
71. K. E. Rehfuess, C. Bosch, and E. Pfannkuch, *Commun. Instituti Forestalis Fennias*, *116*, 122 (1983).
72. A. Ahmad, I. Motoki, and Y. Yamada, *Soil Sci. Plant Nutr.*, *33*, 585 (1987).
73. E. S. Fisher and W. Bussler, *Zeitschrift Pflanzenernähr. Bodenk.*, *151*, 295 (1988).
74. L. B. Klein, S. Chandra, and N. I. Mondy, *J. Agric. Food Chem.*, *30*, 754 (1982).
75. H. Dorenstouter, G. A. Pietus, and G. R. Findenegg, *J. Plant Nutr.*, *8*, 1089 (1985).
76. A. I. Robertson, *New Phytol.*, *100*, 173 (1985).
77. C. Hecht-Buchholtz and J. Schuster, *Plant Soil*, *99*, 47 (1987).
78. R. Salinas, A. Cerda, and V. Martinez, *J. Hort. Sci.*, *61*, 343 (1986).
79. D. L. Plucknett and H. B. Sprague (ed.), "*Detecting Mineral Nutrient Deficiencies in Tropical and Temperate Crops*", Westview Tropical Agric. Series, No. 7., Westview Press, Boulder, CO, 1989.

80. G. C. Gerloff and W. H. Gabelman, in *Inorganic Plant Nutrition* (A. Lauchli and R. L. Bieleski, eds.), Encyclopedia of Plant Physiology New Series, Vol. 15B, Springer-Verlag, Berlin, 1983, pp. 453-480.
81. D. A. Sleper, K. P. Vogel, K. H. Asay, and H. F. Mayland, *J. Anim. Sci., 67* (in press).
82. G. Moseley and D. W. Griffiths, *Grass and Forage Sci., 39,* 195 (1984).
83. O. Loew, "*The Physiological Role of Mineral Nutrients in Plants*", U.S. Dept. Agric. Bull. 45 (1903).
84. B. Bernier and M. Brazeau, *Can. J. For. Res., 18,* 1265 (1988).
85. G. Abrahamsen, in *Ecological Impact of Acid Precipitation, Proceedings of an International Conference, Sandefiord, Norway* (D. Drablos and A. Tollan, eds.), The Norwegian Interdisciplinary Research Programme on Acid precipitation effects on forest and fish, 1980, pp. 58-63.
86. G. Roy, L. Robitaille, and G. Gagnon, *Phytoprotection, 66,* 91 (1985).
87. M. Von Kaupenjohann, W. Zech, R. Hantschel, and R. Horn, *Forstwissenschaftliches Central Blatt, 106,* 78 (1987).
88. H. F. Mayland, in *The Ruminant Animal: Digestive Physiology and Nutrition* (D. C. Church, ed.), Prentice-Hall, Englewood Cliffs, NJ, 1988, pp. 511-523, 530.
89. M. Shils, in *Nutrition Reviews: Present Knowledge in Nutrition,* 5th ed., The Nutrition Foundation, Washington, D.C., 1984, pp. 422-438.
90. G. O. Ramseyer, J. T. Brenna, G. H. Morrison, and R. Schwartz, *Anal. Chem., 56,* 402 (1984).
91. R. M. Welch, "Plant Mineral Nutrition," in *McGraw-Hill Yearbook of Science and Technology*, McGraw-Hill Book Co., New York, 1988, p. 323.
92. R. Schwartz, D. L. Grunes, R. A. Wentworth, and E. M. Wien, *J. Nutr., 110,* 1365 (1980).
93. R. Schwartz, H. Spencer, and J. J. Welsh, *Am. J. Clin. Nutr., 39,* 571 (1984).
94. S. R. Wilkinson and D. A. Mays, in *Tall Fescue* (L. P. Bush and R. C. Buckner, eds.), ASA, Madison, WI, 1979, pp. 41-73.
95. S. R. Wilkinson, R. N. Dawson, O. Devine, and J. B. Jones, Jr., *Commun. Soil Sci. Plant Anal., 18,* 1191 (1987).
96. T. P. Hignett, in *The Fertilizer Handbook*, Fertilizer Inst., Washington, D.C., 1982, pp. 1-20.
97. D. W. Johnson, J. M. Kelly, W. T. Swank, D. W. Cole, H. Van Miegroet, J. W. Hornbeck, R. S. Pierce, and D. Van Lear, *J. Environ. Qual., 17,* 418 (1988).
98. K. C. Beeson, "*Geochemistry and the Environment, Vol. 3, Distribution of Trace Elements Related to the Occurrence of Certain Cancers, Cardiovascular Diseases, and Urolithiasis*", National Academy of Science, Washington, D.C., 1978, pp. 59-78.