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# 6 Magnesium

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## 6.1 HISTORICAL INFORMATION

### 6.1.1 DETERMINATION OF ESSENTIALITY

The word ‘magnesium’ is derived from ‘magnesia’ for the Magnesia district in Greece where talc (magnesium stone) was first mined (1,2). However, there are other cities that are also named after the magnesium deposits in local regions (3). In 1808, Sir Humphry Davy discovered magnesium, but named it magnium, because he considered magnesium to sound too much like manganese. However, in time, the word magnesium was adopted (3–6). Twenty years later, magnesium was purified by the French scientist, Bussy (7). The essentiality of magnesium in plants was established nearly 50 years later (around 1860) by scientists such as Knop, Mayer, Sachs, and Salm-Horstmar (4,8,9), and during the period 1904–1912, Willstatter identified magnesium as part of the chlorophyll molecule (3,6). For many years, magnesium was applied unknowingly to agricultural lands through manure applications or as an impurity with other processed fertilizers (10); therefore, incidences of magnesium deficiency were relatively uncommon. One of the first mentions of magnesium deficiency in plants was in 1923 on tobacco and was referred to as ‘sand drown,’ since the environmental conditions that were associated with magnesium deficiency occurred in excessively leached sandy soils (11). Over 100 years later, magnesium has become a global concern, as scientists suggest that magnesium deficiency may be one of the major factors causing forest decline in Europe and North America (12–17). This malady may be an indirect result of the acidification of soils by acid rain, which can cause leaching of magnesium as well as other alkali metals.

Magnesium is also an essential nutrient for animals. If forage crops, commonly grasses, are low in magnesium, grazing animals may develop hypomagnesemia, sometimes called grass tetany. For this reason, many studies have been conducted on magnesium nutrition in forage crops, in an effort to prevent this disorder (18–24). Based on the review of fertilizer recommendations for field soils in the Netherlands by Henkens (25), the magnesium requirement for forage crops is closely associated with the concentration of potassium and crude protein in the crop. This relationship of magnesium with potassium and crude protein (nitrogen) for animal nutrition is not much different from the magnesium-potassium-nitrogen associations in plant nutrition.

## 6.2 FUNCTION IN PLANTS

### 6.2.1 METABOLIC PROCESSES

Magnesium has major physiological and molecular roles in plants, such as being a component of the chlorophyll molecule, a cofactor for many enzymatic processes associated with phosphorylation, dephosphorylation, and the hydrolysis of various compounds, and as a structural stabilizer for various nucleotides. Studies indicate that 15 to 30% of the total magnesium in plants is associated with the chlorophyll molecule (26,27). In citrus (*Citrus volkameriana* Ten. & Pasq.), magnesium deficiency was associated directly with lower total leaf chlorophyll (28); however, there were no effects on chlorophyll *a/b* ratios within the magnesium-deficient leaves.

The other 70 to 85% of the magnesium in plants is associated with the role of magnesium as a cofactor in various enzymatic processes (1,2,26,29), the regulation of membrane channels and receptor proteins (30,31), and the structural role in stabilizing proteins and the configurations of DNA and RNA strands (32,33). Since magnesium is an integral component of the chlorophyll molecule and the enzymatic processes associated with photosynthesis and respiration, the assimilation of carbon and energy transformations will be affected directly by inadequate magnesium. In nutrient film-grown potato (*Solanum tuberosum* L.), relatively low (0.05 mM) or high (4.0 mM) magnesium concentrations increased dark respiration rates and decreased photosynthetic rates relative to magnesium fertilization rates ranging from 0.25 to 1.0 mM (34). In hydroponically grown sunflower (*Helianthus annuus* L.), photosynthetic rates decreased in ammonium-fertilized, but not nitrate-fertilized plants when the magnesium concentration of nutrient solutions decreased below 2 mM (35). This effect was related to the decreased enzymatic activity as well as the decrease in photosynthetic capacity due to the loss in assimilating leaf area, occurring mainly as a consequence of leaf necrosis and defoliation (36).

Magnesium may also influence various physiological aspects related to leaf water relations (37,38). In hydroponically grown tomato (*Lycopersicon esculentum* Mill.), increasing magnesium fertilization from 0.5 to 10 mM resulted in an increase in leaf stomatal conductance ( $G_s$ ) and turgor potential ( $\Psi_p$ ) and a decrease in osmotic potential ( $\Psi_\pi$ ) but had no effect on leaf water potential ( $\Psi_w$ ) (37). In other studies (38) where low leaf water potentials were induced in sunflower (*Helianthus annuus* L.) leaves, the increased magnesium concentrations in the stroma, caused by decreased stroma volume due to dehydration, caused magnesium to bind to the chloroplast-coupling factor, thereby inhibiting the ATPase activity of the enzyme and inhibiting photophosphorylation. Other experiments (39–41) have indicated that even though up to 1.2 mM magnesium may be required in the ATPase complex of photophosphorylation, magnesium concentrations of 5 mM or higher result in conformational changes in the chloroplast-coupling factor, which causes inhibition of the ATPase enzyme.

As regards to the role of magnesium in molecular biology, magnesium is an integral component of RNA, stabilizing the conformational structure of the negatively charged functional groups and also concurrently neutralizing the RNA molecule (42–44). In many cases, the role of the magnesium ion in the configurations and stabilities of many polynucleotides is not replaceable with other cations, since the ligand configurations are of a specific geometry that are capable of housing only magnesium ions (45). In addition, magnesium serves as a cofactor for enzymes that catalyze the hydrolysis and formation of phosphodiester bonds associated with the transcription, translation, and replication of nucleic acids (1,2).

### 6.2.2 GROWTH

Magnesium deficiency may suppress the overall increase in plant mass or specifically suppress root or shoot growth. However, the extent of growth inhibition of roots and shoots will be influenced by the severity of the magnesium deficiency, plant type, stage of plant development, environmental conditions, and the general nutritional status of the crop. In tomato, suboptimal magnesium concentrations did not affect overall plant growth (37); however, an accumulation of assimilates occurred in the shoots, suggesting that assimilate transport from the shoots to the roots was impaired. For birch (*Betula pendula* Roth.) seedlings, decreased magnesium availability in the rhizosphere had no effect on root branching pattern but decreased root length, root diameter, and root dry weight (36). In addition, the fraction of dry matter allocated to the leaves increased even though overall leaf area decreased (36). In raspberry (*Rubus* spp. L.), enhanced shoot growth was correlated with increased magnesium in the leaves (46,47).

### 6.2.3 FRUIT YIELD AND QUALITY

Magnesium deficiencies and toxicities may decrease fruit yield and quality. In two cultivars of apple (*Malus pumila* Mill.), fruit magnesium concentrations were correlated negatively with fruit color, whereas fruit potassium concentrations were positively correlated with fruit color (48). The effects

of magnesium on apple fruit quality may have been due to antagonistic effects on potassium uptake and accumulation. In tomato, even though increasing magnesium fertilization rates did not affect total shoot dry weight, overall fruit yield decreased with increased magnesium fertilization supply from 0.5 to 10 mM (37).

### 6.3 DIAGNOSIS OF MAGNESIUM STATUS IN PLANTS

#### 6.3.1 SYMPTOMS OF DEFICIENCY AND EXCESS

##### 6.3.1.1 Symptoms of Deficiency

In a physiological sense, magnesium deficiency symptoms are expressed first as an accumulation of starch in the leaves (49), which may be associated with early reductions in plant growth and decreased allocation of carbohydrates from leaves to developing sinks (50). This process is followed by the appearance of chlorosis in older leaves, patterns of which can be explained by the physiological processes associated with magnesium uptake, translocation, and metabolism in plants (3–5,49). Magnesium is physiologically mobile within the plant. Therefore, if insufficient magnesium is available from the rhizosphere, magnesium can be reallocated from other plant parts and transported through the phloem to the actively growing sinks. Because of this mobility within the plant, symptoms of deficiency will first be expressed in the oldest leaves (Figure 6.1). Early symptoms of magnesium deficiency may be noted by fading and yellowing of the tips of old leaves (49,51,52), which progresses interveinally toward the base and midrib of leaves, giving a mottled or herringbone appearance (52). In later stages of development, deficiency symptoms may be difficult to distinguish from those of potassium deficiency. Under mild deficiencies, a 'V'-patterned interveinal chlorosis develops in dicots as a result of magnesium dissociating from the chlorophyll, resulting in chlorophyll degradation. In conifers, minor magnesium deficiency symptoms are browning of older needle tips (0.10% magnesium concentration) and in more severe deficiencies, the entire needle turns brown and senesce (0.07% magnesium concentration) (49,53). In some plants, a reddening of the leaves may occur, rather than chlorosis, as is the case for cotton (*Gossypium* spp.) (52,54), since other plant pigments may not break down as quickly as chlorophyll. The loss of protein from magnesium-deficient leaves, however, usually results in the loss of plastic pigments from most plants (55). On an individual leaf, as well as on a whole plant basis, deficiency



**FIGURE 6.1** Symptoms of magnesium deficiency on (left) pepper (*Capsicum annum* L.) and (right) cucumber (*Cucumis sativus* L.). (Photographs by Allen V. Barker.) (For a color presentation of this figure, see the accompanying compact disc.)

symptoms may begin to appear only on the portions of a leaf or the plant that are exposed to the sun, with the shaded portions of leaves remaining green (49,56). Under severe deficiency symptoms, all lower leaves become necrotic and senesce (28,36) with symptoms of interveinal yellowing progressing to younger leaves (36,56).

Magnesium has functions in protein synthesis that can affect the size, structure, and function of chloroplasts (26). The requirement of magnesium in protein synthesis is apparent in chloroplasts, where magnesium is essential for the synthesis and maintenance of proteins in the thylakoids of the chlorophyll molecule (57–59). Hence, the degradation of proteins in chloroplasts in magnesium-deficient plants may lead to loss of chlorophyll as much as the loss of magnesium for chlorophyll synthesis.

On a cellular level, magnesium deficiency causes the formation of granules of approximately 80 nm in diameter in the mitochondria and leads to the disruption of the mitochondrial membrane (60). In the chloroplasts, magnesium deficiency results in reduced and irregular grana and reduced or nonexistent compartmentation of grana (61). Palomäki (53) noted that chloroplasts were rounded and thylakoids were organized abnormally in magnesium-deficient Scots pine (*Pinus sylvestris* L.) seedlings. In the vascular system, magnesium deficiency may cause swelling of phloem cells and collapse of surrounding cells, collapse of sieve cells, and dilation of proximal cambium and parenchyma cells in conifers (53). These alterations at the cellular level occurred before visual changes were evident and before a detectable decrease in leaf magnesium occurred.

### 6.3.1.2 Symptoms of Excess

During the early 1800s, symptoms of ‘magnesium’ toxicity in plants were described; however, during this time, manganese was called magnesium and magnesium was referred to as magnium or magnesia (3–5). Because of the confusion in nomenclature, early reports regarding magnesium and manganese should be read carefully. At the present time, no specific symptoms are reported directly related to magnesium toxicity in plants. However, relatively high magnesium concentrations can elicit deficiency symptoms of other essential cations. Plant nutrients that are competitively inhibited for absorption by relatively high magnesium concentrations include calcium and potassium and occasionally iron (62). Therefore, symptoms of magnesium toxicity may be more closely associated with deficiency symptoms of calcium or potassium.

### 6.3.2 ENVIRONMENTAL CAUSES OF DEFICIENCY SYMPTOMS

Conditions of the soil and rhizosphere such as drought or irregular water availability (63,64), poor drainage or excessive leaching (11), low soil pH (65–67), or cold temperatures (68,69) will exaggerate magnesium deficiency symptoms, as magnesium is not physically available under these environmental conditions or physiologically, the plant roots are not capable of absorbing adequate magnesium to sustain normal plant growth.

Conditions of the soil and rhizosphere such as drought or irregular water availability will impact magnesium uptake. In sugar maple (*Acer saccharum* Marsh.), foliar analysis indicated that magnesium deficiency occurred during drought (64). Likewise, Huang (63) reported that drought-stressed tall fescue (*Festuca arundinacea* Schreb.) had lower leaf magnesium concentrations than well-watered fescue.

Low soil pH is also associated with a low supply or depletion of magnesium, possibly due to leaching; however, research suggests that impairment of root growth in acid soils (pH 4.3 to 4.7) also may hinder magnesium absorption (67). In one study (65), low soil pH (3.0) resulted in increased accumulation of magnesium in the shoots, but decreased accumulation in the roots. Contradicting Marler (65) and Tan et al. (67), Johnson et al. (70) found no clear correlation between low soil pH and magnesium accumulation.

Relatively high and low root-zone temperatures affect magnesium uptake, but the degree of impact may be influenced by plant type and stage of plant development. Huang et al. (71) and

Huang and Grunes (68) reported that increasing root-zone temperature (10, 15, 20°C) linearly increased magnesium accumulation by wheat seedlings that were less than 30 days old but suppressed accumulation by seedlings that were more than 30 days old. Similarly, magnesium uptake decreased when temperatures in the rhizosphere decreased from 20 to 10°C (69).

Although any environmental condition such as unfavorable soil temperature or pH may reduce root growth and thus reduce magnesium uptake, other characteristics such as mycorrhizal colonization can increase magnesium uptake. Likewise, it has been shown that plants that have colonization of roots by mycorrhiza show higher amounts of magnesium accumulation relative to nonmycorrhizal plants (72–75).

Shoots exposed to environmental parameters such as high humidity (76), high light intensity (77,78), or high or low air temperatures (79) will decrease the ability of plants to absorb and translocate magnesium, since transpiration is reduced and the translocation of magnesium is driven by transpiration rates (63,76,80–84).

Light intensity can affect the expression of symptoms of magnesium deficiency. Partial shading of magnesium-deficient leaves has been shown to prevent or delay the development of chlorosis (77). Others (49,56) have also determined that magnesium deficiency symptoms may begin to appear only on the portions of a leaf or plant that are exposed to the sun, with the shaded portions of leaves remaining green. Zhao and Oosterhuis (78) also reported that shading (63% light reduction) increased leaf-blade concentrations of magnesium in cotton plants by 16% relative to unshaded plants.

### 6.3.3 NUTRIENT IMBALANCES AND SYMPTOMS OF DEFICIENCY

Magnesium deficiency symptoms may be associated with an antagonistic relationship between magnesium ions ( $Mg^{2+}$ ) and other cations such as hydrogen ( $H^+$ ), ammonium ( $NH_4^+$ ), calcium ( $Ca^{2+}$ ), potassium ( $K^+$ ), aluminum ( $Al^{3+}$ ), or sodium ( $Na^+$ ). The competition of magnesium with other cations for uptake ranges from highest to lowest as follows:  $K > NH_4^+ > Ca > Na$  (85,86). These cations can compete with magnesium for binding sites on soil colloids, increasing the likelihood that magnesium will be leached from soils after it has been released from exchange sites. Within the plant, there are also antagonistic relationships between other cations and magnesium regarding the affinity for various binding sites within the cell membranes, the degree of which is influenced by the type of binding site (lipid, protein, chelate, etc.), and the hydration of the cation (87). These biochemical interactions result in competition of other cations with magnesium for absorption into the roots and translocation and assimilation in the plant (88–92).

#### 6.3.3.1 Potassium and Magnesium

Increased potassium fertilization or availability, relative to magnesium, will inhibit magnesium absorption and accumulation and vice versa (34,35,90,93–99). The degree of this antagonistic effect varies with potassium and magnesium fertilization rates, as well as the ratio of the two nutrients to one another. This phenomenon has been documented in tomato (62,96), soybean (*Glycine max* Merr.), (93,100), apple (101), poplar (*Populus trichocarpa* Torr. & A. Gray) (102), Bermuda grass (*Cynodon dactylon* Pers.) (103–105), perennial ryegrass (*Lolium perenne* L.) (18), buckwheat (*Fagopyrum esculentum* Moench) (93), corn (*Zea mays* L.) (98), and oats (*Avena sativa* L.) (93). Potassium chloride fertilization increased cotton (*Gossypium hirsutum* L.) plant size and seed and lint weight and increased efficiency of nitrogen use, but had suppressive effects on magnesium accumulation in various plant parts (106). Fontes et al. (107) reported that magnesium concentrations of potato (*Solanum tuberosum* L.) petioles declined as potassium fertilization with potassium sulfate increased from 0.00 to 800 kg K ha<sup>-1</sup>. Legget and Gilbert (100) noted that with excised roots of soybean, magnesium uptake was inhibited if calcium and potassium were both present but not if calcium or potassium was present alone. The opposite also holds true in that potassium and calcium contents of roots were

depressed with increasing rates of magnesium fertilization (100). Similar results were obtained in potatoes (*Solanum tuberosum* L.) where increasing magnesium fertilization from 0.05 to 4.0 mM decreased the potassium concentration in shoots from 76.6 to 67.6 mg g<sup>-1</sup> shoot dry weight (34).

### 6.3.3.2 Calcium and Magnesium

High rhizosphere concentrations of calcium, relative to magnesium, are inhibitory to the absorption of magnesium and vice versa (34,35,37,86,90,108–110). In the early 1900s, the importance of proper ratios of magnesium to calcium in soils was emphasized through studies conducted by Loew and May (4) on the relationships of lime and dolomite. High calcium concentrations in solution or in field soils sometimes limit magnesium accumulation and may elicit magnesium deficiency symptoms (111–113). In tomato, the magnesium concentration in shoots (62) and fruits (114) decreased as the calcium fertilization rate increased. Similarly, it was shown that increased calcium concentrations inhibited magnesium uptake in common bean (*Phaseolus vulgaris* L.) (86). On the other hand, decreased accumulation of calcium in birch was directly correlated with the decreased absorption and accumulation of calcium as magnesium fertilization rates increased (36). The absorption of calcium decreased from 1.5 to 0.3 mmol g<sup>-1</sup> root mass as magnesium fertilization increased (36). Morard et al. (115) reported a strong antagonism between calcium and magnesium, suggesting that calcium influenced magnesium translocation to leaves. Optimum leaf Ca/Mg ratios are considered to be approximately 2:1; however, Ca/Mg ratios >1:1 and <5:1 can produce adequate growth without the expression of magnesium deficiency (36,85). In a study with tomato, the root, stem, and leaf calcium concentrations decreased as fertilization rates increased from 0.50 to 10.0 mM Mg in solution culture (37). Similarly, with woody ornamentals, high fertilization rates of calcium relative to magnesium inhibited the accumulation of magnesium and decreased root and shoot growth, and inversely, high magnesium decreased calcium accumulation and plant growth (35,109). Clark et al. (116) used flue-gas desulfurization by-products to fertilize corn in greenhouse experiments. They noted that the materials needed to be amended with magnesium at a ratio of 1 part magnesium to 20 parts of calcium to avoid magnesium deficiency in the corn. In containerized crop production, general recommendations indicate sufficient calcium and magnesium additions to produce an extractable Ca/Mg ratio of 2:5 (117). Navarro et al. (118) reported an antagonist effect of calcium on magnesium accumulation in melon (*Cucumis melo* L.), regardless of salinity levels imposed by sodium chloride. In other studies (119–121), it was shown that even with the use of dolomitic lime, magnesium deficiency might occur. This occurrence is due to the different solubilities of magnesium carbonate (MgCO<sub>3</sub>) and calcium carbonate (CaCO<sub>3</sub>) in the dolomite. Therefore, during the first 4 months, both magnesium and calcium solubilized from the dolomite. However, after 4 months, all of the magnesium had dissolved from the dolomite, leaving only Ca from the CaCO<sub>3</sub> available for dissolution and availability to the plant (119,120). Based on these studies, it appears that the use of solid calcium and magnesium fertilizers with similar solubility rates may be important so that both elements are available in similar and sufficient levels throughout the entire crop production cycle (119–121).

### 6.3.3.3 Nitrogen and Magnesium

Nitrogen may either inhibit or promote magnesium accumulation in plants, depending on the form of nitrogen: with ammonium, magnesium uptake is suppressed and with nitrate, magnesium uptake is increased (35,101,122–124). In field soils, the chances of ammonium competing with magnesium for plant uptake are more likely to occur in cool rather than warm soils because in warmer soils, most ammonium is converted into nitrate by nitrification processes. In forests, high inputs of ammoniacal nitrogen amplified latent magnesium deficiency (125). In conditions of sand culture, ammonium-nitrogen of Norway spruce (*Picea abies* Karst.) resulted in significantly lower magnesium and chlorophyll concentrations in current-year and year-old needles compared to fertilization with

nitrate-nitrogen (126). Similarly, in herbaceous plants such as wheat (*Triticum aestivum* L.) (127) and bean (*Phaseolus vulgaris* L.) (128), ammoniacal nitrogen reduced shoot accumulation of magnesium (127). In cauliflower (*Brassica oleracea* var. *botrytis* L.), increasing nitrate-nitrogen fertilization from 90 to 270 kg ha<sup>-1</sup> increased yield response to increased magnesium fertilization rates (22.5 to 90 kg ha<sup>-1</sup>) (129). Similarly, in hydroponically grown poinsettia (*Euphorbia pulcherrima* Willd.), magnesium concentrations in leaves increased as the proportion of nitrate-nitrogen to ammonium-nitrogen increased, even though all treatments received the same amount of total nitrogen (130). In a similar way, magnesium fertilization increased the plant accumulation of nitrogen, which was applied as urea, in rice (*Oryza sativa* L.) (131). As with other nutrients, the degree of impact of nitrogen on magnesium nutrition is influenced by the concentrations of the nutrients, relative to each other. For example, Huang et al. (71) demonstrated with hydroponically grown wheat that nitrogen form had no significant effect on shoot magnesium levels when magnesium concentrations in solutions were relatively high (97 mg L<sup>-1</sup>); however, at low magnesium concentrations (26 mg L<sup>-1</sup>) in solutions, increasing the proportion of ammonium relative to nitrate significantly decreased shoot Mg concentrations. In another study, Huang and Grunes (68) also noted that even though magnesium uptake rates were significantly higher for plants supplied with nitrate rather than ammonium, increasing the proportion of the nitrogen supply as nitrate decreased net magnesium translocation to the shoots.

#### 6.3.3.4 Sodium and Magnesium

High soil or nutrient-solution salinity levels (with NaCl), relative to magnesium supply, may inhibit magnesium accumulation in plants (132–135). However, results are variable since salinity often inhibits plant growth; therefore, there may be a reduction in the total uptake of a nutrient into a plant. However, since the plant is smaller, the magnesium level, expressed in terms of concentration, may be higher. Application of sodium-containing fertilizers (chloride or nitrate) lowered the concentration of magnesium in white clover (*Trifolium repens* L.) leaves but increased the magnesium in perennial ryegrass (*Lolium perenne* L.) (133). In hydroponically grown taro (*Colocasia esculenta* Schott.) (136) and wheat (137), sodium chloride treatments resulted in a suppression of leaf magnesium. Use of sodium chloride to suppress root and crown rot in asparagus (*Asparagus officinalis* L. var. *altilis* L.) also suppressed magnesium accumulation in the leaves (138). Even in a halophyte such as *Halopyrum mucronatum* Stapf., increasing sodium chloride concentrations in nutrient solutions from 0.0 to 5220 mg L<sup>-1</sup> significantly decreased magnesium concentrations in the shoots and roots (134). However, in hydroponically grown bean (*Phaseolus vulgaris* L.), sodium chloride increased leaf concentrations of magnesium, perhaps as a result of growth suppression (139). Growth suppression of rice was associated with salinity, but the levels of magnesium in the leaves were unaffected (140). Other research (141) found that sodium chloride increased accumulation of magnesium in shoots but suppressed magnesium accumulation in roots of strawberry (*Fragaria chiloensis* Duchesne var. *ananassa* Bailey). In fact, some (142) have attributed the salt tolerance of some soybean cultivars to the ability to accumulate potassium, calcium, and magnesium, in spite of saline conditions.

#### 6.3.3.5 Iron and Magnesium

Uptake and accumulation of iron may be inhibited or unaffected by increased magnesium fertilization. In addition, the translocation of magnesium from the roots to the shoots may decrease in iron-deficient plants relative to iron-sufficient plants (143). The antagonistic relationship of iron with magnesium has been demonstrated in tomato (62) and radish (*Raphanus sativus* L.) (144). Nenova and Stoyanov (143) noted that the uptake and translocation of magnesium was reduced in iron-deficient plants compared to iron-sufficient plants. However, Bavaresco (145) reported that under lime-induced chlorosis, chlorotic grape (*Vitis vinifera* L.) leaves did not differ from green leaves in nutrient composition, but the fruits of chlorotic plants were different in that they had higher magnesium than fruits from normal plants. Iron concentrations did not differ among any of the tissues.



### 6.3.3.6 Manganese and Magnesium

Manganese, as a divalent cation, can compete with magnesium for binding sites on soil particles as well as biological membranes within plants (146). However, manganese is required in such small quantities (micromolar concentrations in nutrient solutions resulting in Manganese, as a divalent cation, can compete with magnesium for binding sites on soil particles as well as biological membranes within plants (146). However, manganese is required in such small quantities (micromolar concentrations in nutrient solutions resulting in  $\approx 20$  to 500 ppm in most plant tissues) that manganese toxicity usually occurs before quantities are high enough to significantly inhibit magnesium uptake to physiologically deficient levels (62,85). However, some experiments (147,148) have demonstrated that manganese can inhibit magnesium uptake. However, Alam et al. (147) and Qauartin et al. (148) did not indicate if the inhibition of magnesium was substantial enough to induce magnesium deficiency symptoms. On the other hand, increased magnesium fertilization has been shown to decrease manganese uptake and accumulation (34,80), and in some cases, magnesium fertilization may mitigate manganese toxicity (149,150). In one study (151), the tolerance of certain cotton (*Gossypium hirsutum* L.) cultivars to manganese appeared to be related to the ability to accumulate more magnesium than by the manganese-sensitive cultivars.

### 6.3.3.7 Zinc and Magnesium

As with manganese, zinc is a divalent cation that is required in minuscule quantities for normal plant growth. Therefore, plants usually suffer from zinc toxicity before concentrations are high enough to inhibit magnesium uptake. However, some research has indicated that as zinc increases to toxic levels in plants, the accumulation of magnesium is suppressed, but not to the degree of inducing magnesium deficiency symptoms. In hydroponically grown tomato (62), increasing zinc concentrations from 0.0 to 1.58 mg L<sup>-1</sup> did not affect magnesium concentrations in shoots. Similarly, nontoxic levels of zinc applications through zinc-containing fungicides or fertilization (soil or foliar applied) did not affect magnesium concentrations in potato leaves, although zinc concentrations increased in leaves (152). However, at higher zinc concentrations (30 vs. 0.5 mg L<sup>-1</sup>), magnesium accumulation in tomato leaves and fruit was inhibited (153). Similarly, with blackgram (*Vigna mungo* L.) grown in soil, accumulation of zinc in plants led to a suppression of magnesium, calcium, and potassium in leaves (154). Bonnet et al. (155) also reported that zinc fertilization of ryegrass (*Lolium perenne* L.) lowered magnesium content of leaves, in addition to lowering the efficiency of photosynthetic energy conversion, and elevating the activities of ascorbate peroxidase and superoxide dismutase. Conversely, pecan (*Carya illinoensis* K. Koch) grown under zinc-deficient conditions had higher leaf magnesium than trees grown under zinc-sufficient conditions (156). However, in nutrient film-grown potatoes (*Solanum tuberosum* L.), increased levels of magnesium fertilization (1.2 to 96.0 mg L<sup>-1</sup>) did not affect zinc concentrations in tissues.

### 6.3.3.8 Phosphorus and Magnesium

Phosphate ions have a synergistic effect on accumulation of magnesium in plants, and vice versa. This phenomenon is associated with the ionic balance related to cation and anion uptake into plants as well as the increased root growth sometimes observed with increased phosphorus fertilization. For example, with hydroponically grown sunflower (*Helianthus annuus* L.), phosphorus accumulation increased in tissues from 9.0 to 13.0 mg g<sup>-1</sup> plant dry weight as magnesium concentrations in nutrient solutions were increased from 0.0 to 240 mg L<sup>-1</sup> (35). Likewise, increasing phosphorus fertilization increases magnesium accumulation, as demonstrated in field-grown alfalfa (*Medicago sativa* L.) (157). The effect of phosphorus fertilization increasing magnesium uptake has also been documented in rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), bean (*Phaseolus vulgaris* L.), and corn (*Zea mays* L.) (158). Reinbott and Blevins (82,159) reported that phosphorus fertilization of field-grown wheat (*Triticum aestivum* L.) and tall fescue (*Festuca arundinacea* Shreb.) increased

leaf calcium and magnesium accumulation and concluded that proper phosphorus nutrition may be more important than warm root temperatures in promoting magnesium and calcium accumulation, particularly if soils have suboptimal phosphorus concentrations. Reinbott and Blevins (160) also showed a positive correlation between calcium and magnesium accumulation in shoots with increased phosphorus fertilization of hydroponically grown squash (*Cucurbita pepo* L.).

### 6.3.3.9 Copper and Magnesium

Like other micronutrients, copper is a plant nutrient, which is required in such low concentrations relative to the requirements for magnesium that high copper fertilization is more likely to induce copper toxicity before causing magnesium deficiency symptoms. However, some studies have shown that copper may competitively inhibit magnesium accumulation in plants (161,162). In taro (*Colocasia esculenta* Schott), increasing the nutrient solution copper concentrations from 0.03 to 0.16 mg L<sup>-1</sup>, significantly decreased the accumulation of magnesium in leaves from 5.5 to 4.4 mg g<sup>-1</sup> dry weight (161). In a study (162) using young spinach (*Spinacia oleracea* L.), where copper concentrations in nutrient solutions were increased from 0.0 to 10.0 mg L<sup>-1</sup>, which is two orders of magnitude greater than the copper concentrations used in the study conducted by Hill et al. (2000), copper toxicity symptoms did occur, and there was a significant suppression in magnesium accumulation in the leaves and roots from 322 and 372 mg kg<sup>-1</sup> to 41 and 203 mg kg<sup>-1</sup>, respectively (162). However, the magnesium concentration reported in this study (162) is an order of magnitude lower than what is found typically in most herbaceous plants (85). On the other hand, effects of magnesium fertilization on copper uptake are not documented, although one study (34) indicated that increasing rates of magnesium fertilization did not significantly reduce the uptake and accumulation of copper.

### 6.3.3.10 Chloride and Magnesium

The effects of chloride on magnesium accumulation in plants have been studied in relation to the effects of salinity on growth and nutrient accumulation. In many of these studies, it is difficult to separate the effects of chloride from those of sodium ions; hence, many of the results show a depression of magnesium accumulation with increases in sodium chloride concentration in the root zone (132–135). In grapes (*Vitis vinifera* L.), salinity from sodium chloride did not affect magnesium concentrations in leaves, trunk, or roots (163). With tomato, increased magnesium fertilization rates did not increase the accumulation of chlorine in the leaves, stems, or roots (37). With soybean, uptake of chloride by excised roots was low from magnesium chloride solutions but was enhanced by the addition of potassium chloride (100).

### 6.3.3.11 Aluminum and Magnesium

Free aluminum in the soil solution inhibits root growth, which in turn will reduce ability of plants to take up nutrients (164). Research with red spruce (*Picea rubens* Sarg.) indicated that magnesium concentrations in roots and needles of seedlings were suppressed by exposure to  $\approx 400 \mu\text{M}$  aluminum in nutrient solutions (165,166). Increasing concentrations of free aluminum have also been shown to reduce magnesium accumulation in taro (167), maize (*Zea mays* L.) (168,169), and wheat (*Triticum aestivum* L.) (170). Aluminum-induced magnesium deficiency may be one mechanism of expression of aluminum toxicity in plants, and aluminum tolerance of plants may be related to the capacity of plants to accumulate magnesium and other nutrients in the presence of aluminum (67,95,168,170–172). Some studies (173) have shown that the toxic effects of aluminum were reduced when magnesium was introduced into the nutrient solution and subsequently increased the production and excretion of citrate from the root tips. The authors (173) hypothesized that the citrate binds with free aluminum, forming nontoxic aluminum–citrate complexes. Keltjens (168) also reported that aluminum chloride in solution culture restricted magnesium absorption by corn

but that aluminum citrate or organic complexes did not inhibit magnesium absorption and were not phytotoxic.

Sensitivity to aluminum toxicity may or may not be cultivar-specific. In a study (170) with wheat, differences in magnesium accumulation occurred for different cultivars, with a significantly greater accumulation of magnesium in the leaves of the aluminum-tolerant 'Atlas 66' compared to the aluminum-sensitive 'Scout 66' and increasing the magnesium concentration in nutrient solutions relative to aluminum and potassium concentrations increased the aluminum tolerance of 'Scout 66' (170). However, in another study (174) with aluminum-tolerant and aluminum-sensitive corn cultivars, increasing concentrations of aluminum resulted in higher nutrient concentrations in the shoots of aluminum-sensitive than in the aluminum-tolerant cultivar, probably the result of a greater suppression of growth in the sensitive cultivar.

#### 6.3.4 PHENOTYPIC DIFFERENCES IN ACCUMULATION

The uptake and accumulation of magnesium may change during different stages of physiological development. Knowledge of these changes is important in managing nutritional regimes for plant growth and for sampling of plants to assess their nutritional status. In poinsettias, magnesium accumulation was greatest from the period of flower induction to the visible bud stage, but then accumulation decreased during the growth phase of visible bud to anthesis (130). With cotton (*Gossypium hirsutum* L.), maximum daily influx of magnesium into roots occurred at peak bloom (175). Accumulation (net influx) of magnesium in annual ryegrass (*Lolium multiflorum* Lam.) decreased with increasing plant age (176,177). Similarly, magnesium uptake rates by tomato decreased from 68 to 17.5  $\mu\text{eq g}^{-1}$  fresh weight per day as the plants aged from 18 to 83 days (110). With anthurium (*Anthurium andraeanum* Lind.), changes in the allocation of magnesium to different organs with increased plant age were attributed to transport of nutrients from lower leaves to the flowers, resulting in a lowering of magnesium concentrations in the lower leaves (178). Tobacco (*Nicotiana tabacum* L.) showed decreasing concentrations of leaf magnesium from base to top of the plants over the growing season, and stem magnesium concentrations also fell with plant age (179). Sadiq and Hussain (180) attributed the decline in magnesium concentration in bean (*Phaseolus vulgaris* L.) plants to a dilution effect from plant growth. However, Jiménez et al. (181) reported no significant differences in shoot-tissue magnesium concentrations throughout the different growth stages of different soybean cultivars.

#### 6.3.5 GENOTYPIC DIFFERENCES IN ACCUMULATION

Variation in magnesium accumulation might occur for different cultivars or plant selections within a species. In a 2-year study with field-grown tomato plants in an acid soil, magnesium concentration of leaves was significantly greater in cultivar 'Walter' (1.1%) than in 'Better Boy' (0.9%) in a dry, warm year, but no differences (average 0.6%) occurred between the cultivars in a wetter, cooler year that followed (182). Mullins and Burmester (183) noted that cotton cultivars differed in concentrations of magnesium in leaves and burs under nonirrigated conditions. Differences in magnesium concentrations in different cultivars of Bermuda grass (*Cynodon dactylon* Pers.) have been reported (184). Rosa et al. (185) suggested that variation in calcium, magnesium, and sulfur among broccoli (*Brassica oleracea* var. *italica* Plenck) varieties justifies selection of a particular cultivar to increase dietary intake of these elements. Likewise, in different wheat (*Triticum aestivum* L.) (170) and barley (*Hordeum vulgare* L.) (171) cultivars, aluminum tolerance was associated with the ability to take up and accumulate magnesium under conditions of relatively high aluminum concentrations (1.35 to 16.20  $\text{mg L}^{-1}$ ) in the rhizosphere. Similar studies (94) have been conducted to select clonal lines of tall fescue (*Festuca arundinacea* Schreb.), which display higher accumulation of magnesium, in an effort to prevent magnesium tetany in grazing animals.