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REGULAR ARTICLE

The role of magnesium in plant disease

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Abstract
Background Magnesium (Mg), as an essential mineral element for plants and microbes, can have both indirect as well as direct effects on disease. Balanced nutrition is critical for the expression of disease resistance since nutrition is part of a delicately balanced interdependent system influenced by the plant's genetics and the environment. A deficiency or excess of Mg can influence a wide range of physiologic functions because of these interrelated processes.
Scope There are fewer reports of direct effects of Mg deficiency or excess on plant disease than for many elements because of its participation in a wide spectrum of general physiological functions so that individual activities involved in defense, virulence, or pathogenesis are not as easily characterized. The ability of Mg to compliment or antagonize other minerals can result in different disease responses to Mg under varying environmental conditions. Fusarium wilt pathogens tend to be less severe when adequate Mg is available, and Mg increases resistance of tissues to degradation by some pectolytic enzymes of macerating or soft rotting pathogens. In contrast, high rates of Mg that interfere with Ca uptake may increase the incidence of diseases such as bacterial spot of tomato and pepper or peanut pod rot.
Conclusions The more general physiological benefits of Mg for active growth often obscure specific mechanisms involved in resistance to disease, although Mg is an important contributor to over-all plant health. A specific mechanism of defense to diseases enhanced by Mg includes increased resistance of tissues to degradation by pectolytic enzymes of bacterial soft rotting pathogens. Management of Mg nutrition to reduce disease, in balance with other minerals, is an underutilized tool for disease control.

Keywords Magnesium · Disease · Pathogens · Pathogenesis · Disease resistance

Introduction

Although this chapter discusses the interactions between Mg and plant disease, it should be recognized that agriculture is the management of an ecological system comprised of major and secondary interacting components. The major components consist of the plant, the abiotic environment, and the biotic environment (Fig. 1). Each of these major components is comprised of various factors that favor or inhibit plant disease. It is the interaction of these various components

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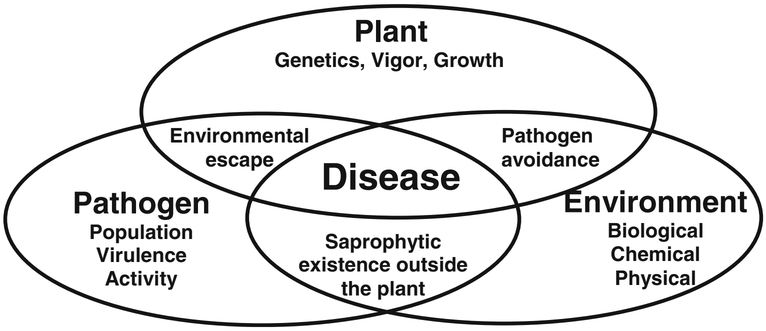
Fig. 1 Schematic of the interacting components managed in the agricultural ecology that determine disease severity, crop productivity, and nutritional status



that determines the health, vigor, productivity and nutritional quality of crops produced. When one factor in the agricultural system is changed, it affects the interactions of others and the influence they have on disease and crop productivity. A common effect of disease is alteration of nutrition, and it is frequently difficult to clearly differentiate between the biotic and abiotic factors that interact to 'cause' a nutrient deficiency or excess (Huber 1978; Huber and Graham 1999). Through altered nutrient uptake, translocation, distribution, and physiological function, many localized and systemic symptoms of pathogenesis are similar to abiotically-induced nutrient deficiencies or excesses (Huber 1989a, b; Huber and Graham 1999).

Nutrition, although frequently unrecognized, always has been a primary component of plant disease control. Nutrient manipulation through fertilization, or modification of the soil environment to influence nutrient availability, is an important cultural control for plant disease and an integral component of production agriculture. Cultural practices used for disease control (such as crop sequence, organic amendment, liming for pH adjustment, tillage, seedbed preparation, and irrigation) frequently influence disease by increasing or decreasing the availability of various mineral nutrients. Integrating the effects of specific mineral nutrients with genetic resistance, sanitation, and cultural practices has provided effective control of many diseases. Magnesium is both a tissue component as well as a regulator of physiological processes in plants that influence the general health status and susceptibility or resistance to disease. There are several general reviews of the relationship between mineral nutrition and plant disease (Datnoff et al. 2007; Engelhard 1989; Graham 1983; Graham and Webb 1991; Huber 1978, 1980, 1981, 1989a, b, 1991; Huber and Graham 1999; Huber and Haneklaus 2007; Jones and Huber 2007; Marschner 2011; McNew 1953). This paper is an update and extension of our chapter on Mg and disease in Datnoff et al. (2007) that has been formatted specifically for this issue of Plant and Soil and the International Symposium on Magnesium in Crop Production, Food Quality and Human Health held at Gottingen, Germany 8–9 May 2012.

Magnesium and plant disease

As a component of the abiotic environment; the rate, source, and availability of Mg has a profound affect on other aspects of this environment, the biological environment, and plant growth and vigor because Mg is an essential mineral element for plants, animals, and microbes (Fulmer 1918; Choi and Carr 1968; Weinberg 1977). An affect of Mg on plant disease has been observed through mineral amendment, comparing Mg concentrations in resistant and susceptible cultivars, comparing concentrations in diseased and healthy cultivars, or correlating conditions affecting Mg availability with disease severity (Jones and Huber 2007; Rogan et al. 2000; Sugawara et al. 1998). It is important to know the over-all nutrient status of the plant in assessing a particular nutrient's effect on plant disease since metabolic systems may respond differently to a particular nutrient depending on other ions present (Cl^-, NO_3^-, $SO_4^=$) (Marschner 2011). Magnesium availability may vary depending on environmental conditions (especially soil pH,), the previous crop, microbial activity in the rhizosphere, herbicide program for weed control, and ratios with other mineral nutrients (especially Ca, K, and Mn). Thus, the effect of Mg on disease may be an indirect effect of Mg on general plant health or a direct effect related to a specific physiological function of this essential mineral element. Since Mg may be applied as different salts (CO_3, Cl, O, NO_3, SO_4, etc.), the anion component of the salt may exert an effect on Mg solubility or its own effect on disease by changing the soil pH

($^{-}CO_3$) or the physiological function of Mg (^{-}Cl, $-NO_3$, $-S$, $-SO_4$) in the plant.

There is less documentation of interactions of Mg with disease than with other nutrients in enhancing or minimizing disease. Jones and Huber (2007) reported 22 diseases that were decreased by supplying additional Mg, 17 that were increased, and 6 where it had a variable effect depending on the environment (Table 1). Some of these different interactions are reflected in the synergy or antagonism of the various nutrients where high levels of K or Ca may inhibit the uptake of Mg just as high levels of Mg inhibit the uptake of K, Mn, and Ca (Persson and Olsson 2000). Plants growing in acid soils tend to be deficient in Mg, Ca, Mo, and P because of impaired absorption of these ions and, therefore, more susceptible to diseases common in low pH soils such as Fusarium wilts, club root of cabbage, and bacterial soft rots (Huber and Graham 1999). Liming the soil with dolomitic lime to increase soil pH also may increase Mg availability to reduce these diseases (Jones et al. 1989).

Mineral nutrient balance is important as evidenced by blossom end rot of tomato that is increased when P, K, and Mg are out of balance with Ca (Anonymous 1999). The reduced concentration of Mg in corn stunt spiroplasma infected maize plants (Ammar and Hogenhouts 2005; Oliveira et al. 2002, 2005) has been considered a competition for Mg between the pathogen and the plant, with more severe symptoms being expressed under low than high Mg conditions; however, Mg may also influence the way the pathogen invades and colonizes plant phloem tissues since it is located inside young phloem cells with high Mg and outside their cells under a Mg deficiency (Nome et al. 2009). Hydrogen ion concentration (pH), Ca, Mg, and cation exchange capacity were the primary factors influencing the composition of *Pythium* in the soil and the severity of disease caused by *Pythium* (Broders et al. 2009).

Indirect effects of magnesium on disease

Most physiological processes affecting plant disease that are influenced by Mg are generally not fully understood. Some of these processes are probably general mechanisms through multiple pathways important for general plant health since Mg is a component of structural tissues and participates in many physiological functions and biochemical processes. Structurally, Mg is a component of the middle lamella and a constituent of the chlorophyll molecule. It is also required for the preservation of ribosome structure and integrity, associated with rapid growth, active mitosis, high protein levels, carbohydrate metabolism, and oxidative phosphorylation. It is involved in energy transfer reactions, respiration, the formation of DNA and RNA, and serves as a cofactor for many enzymes (Marschner 2011). All of these processes are influenced by plant disease and involved with a plant's response to a disease (Horsfall and Cowling 1978, 1980). Increased respiration associated with pathogen penetration and host response requires energy from photosynthesis generated through Mg's role in photosynthesis and subsequent sugar movement. A deficiency of Mg during growth reduces the structural integrity of the middle lamella and the production of energy necessary for defense functions and inactivation of pathogen metabolites. Plants have preformed physical and chemical defenses (Akai and Fukutomi 1980; Schlosser 1980) and active defenses produced after penetration or infection (Beckman 1980), both of which require energy and substrates from photosynthesis involving Mg as a component of the chlorophyll molecule or as a cofactor for the various physiologic processes. Thus, the production of physical and chemical responses to infection requires energy from photosynthesis (Horsfall and Cowling 1980) that is dependent on a sufficiency of Mg.

Mg plays a fundamental role in phloem export of photosynthates so that a deficiency of Mg restricts the partitioning of dry matter between roots and shoots to result in excessive sugar, starch and amino acid accumulation in leaves (source tissues), chlorophyll breakdown, an over-reduction in the photosynthetic electron transport chain and the generation of highly reactive oxygen species (ROS) because of impairment in photosynthetic CO_2 fixation (Cakmak and Kirby 2008; Hermans et al. 2005). A deficiency of Mg can be induced in calcarious soils by competing Ca^{2+} ions, in acid soils by NH^{4+} and Al^{3+}, Na^{+} in saline soils (Mengel and Kirkby 2001), and by the herbicide glyphosate (N-(phosphonomethyl) glycine) (Bott et al. 2008; Eker et al. 2006; Huber 2010; Yamada et al. 2009; Zobiole et al. 2010). These conditions that limit Mg availability are conducive for various diseases (Huber 1978, 1991) and several severe plant diseases such as those caused by mosaic viruses and *Candidatus* Liberibacter spp. are characterized by vascular dysfunction where sucrose and starch accumulate in leaves, and symptoms similar to Mg deficiency

Table 1 Some reported interactions of soil or tissue magnesium with plant diseases

Plant	Disease	Causal agent	Effect of Mg	References
Alfalfa	Mosaic	Alfalfa mosaic virus	Increase	Tu 1978
Apple	Bitter pit	Environmental agents	Increase	Burmeister and Dilley 1993
Apple	Replant disease	Soilborne agents	None	Li and Utkhede 1991
Bean	Root rot	*Rhizoctonia solani*	Decrease	Bateman 1965
Broccoli	Clubroot	*Plasmodiophora brassicae*	Decrease	Myers and Campbell 1985
Cabbage	Clubroot	*Plasmodiophora brassicae*	Decrease	Haenseler 1939
Calendula	Seedling blight	*Pythium aphanidermatum*	Increase	Gill 1972
Carnation	Wilt	*Fusarium oxysporum*	Decrease	Lyakh 1986
Caster bean	Leaf spot	*Botrytis* spp.	Decrease	Thomas and Orellana 1964
Cereals	Stem rust	*Puccinia graminis*	Increase	McNew 1953
Cereals	Stripe rust	*Puccinia striiformis*	Increase	McNew 1953
Citrus	Huanglongbing	*Candidatus* Liberibacter spp.	Decrease	Rouse et al. 2010, 2012
Corn	Stunt	*Spiroplasma kunkelii*	Decrease	Nome et al. 2009; Ammar and Hogenhouts 2005; Oliveira et al. 2002, 2005
Cotton	Bacterial blight	*Xanthomonas campestris* pv. *malvacearum*	Decrease	Batson 1971
Cotton	Damping-off	*Rhizoctonia solani*	Decrease	Tsai and Bird 1975
Cotton	Root rot	*Phymatotrichum omnivorum*	Increase	Bell 1989; Tsai 1974
Cotton	Wilt	*Fusarium oxysporum* f.sp. *conglutinans*	Decrease	National Research Council 1968
Cotton	Wilt	*Verticillium albo-atrum*	Decrease	Batson 1971
Crucifers	Clubroot	*Plasmodiophora brassicae*	Decrease	Young et al. 1991
Grapevine	Dieback	*Eutypa lata*	Decrease	Colrat et al. 1999
Lodgepole pine	Root rot	*Armillaria ostoyae*	None	Mallett and Maynard 1998
Maize	Southern leaf blight	*Bipolaris maydis*	Increase	Taylor 1954
Pea	Root rot	*Aphanomyces euteiches*	None	Persson and Olsson 2000
Peanut	Leaf spot	*Mycosphaerella arachidicola*	Decrease	Bledsoe et al. 1945
Peanut	Pod rot	*Fusarium* spp.	Increase	Halleck and Garren 1968
Peanut	Pod rot	*Pythium myriotylum*	Increase	Csinos and Bell 1989; Halleck and Garren 1968
Peanut	Pod rot	*Rhizoctonia solani*	Increase	Csinos and Bell 1989; Halleck and Garren 1968
Pear	Fire blight	*Erwinia amylovora*	None	Koseoglu et al. 1996
Pepper	Bacterial spot	*Xanthomonas campestris* pv. *vesicatoria*	Increase	Woltz and Jones 1979; Jones et al. 1983
Poppy	Downy mildew	*Peronospora arborescens*	Decrease	Szepessy and Hegedu'sne 1982
Poppy	Mold	*Alternaria* spp., *Capnodium* spp., *Cladosporium* spp.	Decrease	Szepessy and Hegedu'sne 1982
Potato	Early blight	*Alternaria solani*	Decrease	Elfrich 2010
Potato	Gangrene	*Phoma exigua* var. *foveata*	Decrease	Olsson 1984
Potato	Scab	*Streptomyces scabies*	None	Kristufek et al. 2000
Potato	Soft rot	*Erwinia carotovora* pv. *atroseptica*	Decrease	Kelman et al. 1989; McGuire and Kelman 1986; Pagel and Heitfus 1990
Potato	Tuber rot	Various fungi	Decrease	Percival et al. 1999
Rice	Leaf spot	*Helminthosporium* spp.	Decrease	Baba 1958
Rice	Panicle blast	*Pyricularia grisea*	Increase	Filippi and Prabhu 1998

Table 1 (continued)

Plant	Disease	Causal agent	Effect of Mg	References
Rye	Stalk smut	*Urocystis occulta*	Increase	Tapke 1948
Soybean	Root rot	*Rhizoctonia solani*	Decrease	Castano and Kernkamp 1956; Kernkamp et al. 1952
Sugar maple	Decline	Soilborne agent	Decrease	Horsley et al. 2000
Soybean	Twin stem	*Sclerotium* spp.	Increase	Muchovej and Muchovej 1982
Tobacco	Downy mildew	*Peronospora tabacina*	Decrease	Edreva et al. 1984
Tomato	Bacterial speck	*Pseudomonas syringae* pv *tomato*	Increase	Vallad et al. 2003
Tomato	Bacterial spot	*Xanthomonas campestris* pv. *vesicatoria*	Increase	Woltz and Jones 1979
Tomato	Blossom end rot	Nutrient imbalance	Increase	Anonymous 1999
Tomato	Seedling blight	*Pythium myriotylum*	Increase	Gill 1972
Tomato	Wilt	*Fusarium oxysporum*	Increase	Jones et al. 1989
Vicia faba	Chocolate spot	*Botrytis fabae*	Decrease	Rabie 1998
Wheat	Flag smut	*Urocystis tritici*	Increase	Millikan 1939
Wheat	Take-all	*Gaeumannomyces graminis*	Increase	Huber 1981, 1985, 1989a, b
Wheat	Take-all	*Gaeumannomyces graminis*	Variable	Huber and McCay-Buis 1993
Wheat	Wet smut	Unidentified fungus	Decrease	Schutte 1957

Adapted from Jones and Huber 2007

occur. Impaired root absorption of Mg or root dysfunction from necrosis resulting in Mg deficiency could result in a similar accumulation of photosynthates in leaves even though the symptoms expressed by the plant are remote from the cause. The role of Mg in the phloem-loading process seems to be specific so that Mg deficiency results in the accumulation of sucrose and starch in leaves (source tissue) (Cakmak and Kirby 2008).

The accumulation of sucrose and starch in leaf tissue under Mg deficiency could provide a nutrient-dense environment favorable for various pathogens and pests. Increasing concentrations of glucose partially reversed the inhibitory effect of Ca on germination and germ-tube elongation of *Botrytis cinerea* and *Penicillium expansum*, two post harvest rot diseases of apple, although Mg had no direct effect on the pathogens or their macerating enzymes (Wisniewski et al. 1995). Thus, high levels of sugar in tissues under Mg deficiency could reduce the effectiveness of Ca in reducing post harvest losses caused by these two pathogens. The accumulation of sugar and starch in leaves also may result from phloem disruption, tissue maceration, and plugging as observed with vascular wilt diseases and HLB to predispose plants to secondary pathogens. Restoration of phloem function through nutritional amendment can restore photosynthate partitioning to sink tissues and greatly reduce the severity of these diseases. Huanglongbing (HLB) of citrus caused by endogenous phloem-limited *Candidatus* Libibacter spp. is one such disease where infected plants are characterized by the accumulation of sugar and starch in leaves, Zn deficiency, high proline in vascular sap, and impaired phloem function (Bove 2006). Although genetic resistance and chemical controls are not available for this serious disease, citrus production can be maintained through an integrated management plan including foliar applications of Mg and other mineral elements to promote sugar movement and restore phloem function even when 100 % of the trees are infected (Rouse et al. 2010, 2012). In contrast to earlier Chinese research with primarily soil-applied mineral nutrients (Xia et al. 2011), recent HLB-nutrition research in Florida has concentrated on foliar application of minerals within a fully balanced soil nutrient and pest management program. The integrated "Boyd" nutritional amendment program currently practiced in Florida is restoring phloem function to HLB-infected trees (Briansky 2012) and maintaining citrus production (Rouse et al. 2012). It is certainly a better alternative than continued removal of infected trees leading to loss of the citrus industry.

The almost four decade shift of agriculture to a monochemical weed management program using the strong, systemic cationic chelator, N-(phosphonomethyl)glycine (glyphosate, the active ingredient in Roundup® and other herbicides), and genetically engineered plants with tolerance to this herbicide, has resulted in a reduction in Mg uptake efficiency, physiological function, and content of Mg and other cationic mineral nutrients in plants (Cakmak et al. 2009; Eker et al. 2006; Huber 2010; Zobiole et al. 2010) with a subsequent increase in the prevalence and severity of many plant and animal diseases (Huber 2010; Johal and Huber 2009; Yamada et al. 2009) influenced by these mineral nutrients. Although analysis sometimes indicates an adequate level of Mg or other mineral elements in tissues, there is little evidence that once chelated with the systemic glyphosate that they are available for physiological functions (Huber 2010). The accumulation of gyphosate in meristematic tissues (shoot and root tips, legume nodules, cambium, and reproductive structures) reduces the availability of essential elements for active growth to predispose these tissues to both abiotic and biotic diseases. Foliar applications of Mg could be beneficial in 'detoxifying' residual glyphosate in meristems of herbicide-tolerant and non-target plants through its rapid mobility to these tissues and strong chelating ability with glyphosate. Magnesium also can have an important role in detoxifying residual herbicides such as glyphosate that immobilize many micronutrients by chelating with them in soil. Mineral amendment to compensate for reduced nutrient availability has increased plant nutrient content and reduced disease (Huber 2010; Johal and Huber 2009).

Some indirect effects of Mg on plant disease are observed when Mg is in excess of nutrient sufficiency through modification of the environment or interactions with other nutrients. Magnesium deficiency is readily cured by fertilizing with dolomitic lime ($CaCO_3$ + $MgCO_3$) that neutralizes soil acidity and supplies Mg in a form available for plant uptake. The change in soil pH also changes the availability of several micronutrients (Fe, Mn, Zn) to have an indirect effect on disease through reduced availability of these nutrients. As a consequence, Mg often reduces plant diseases generally categorized as "low" rather than "high" pH diseases (Smiley 1975).

Various salts of Mg occur in soil, and interactions with K, Ca, and Mn that modify the availability of other elements are common (James et al. 1995). Magnesium chloride increases Fusarium wilt of tomato caused by *Fusarium oxysporum* f.sp. *lycopersici*, and may counteract the benefit of Ca in reducing this disease (J.P. Jones et al. 1989). Magnesium and K reduce the Ca content of peanut pods and predispose them to pod breakdown caused by *Pythium* and *Rhizoctonia*. The detrimental effects of Mg on *Pythium* and *Rhizoctonia* pod rot have been offset by a concomitant application of gypsum (Csinos and Bell 1989). In contrast, Mg is almost as effective as Ca in preventing maceration of tissues by soft rot pathogens (Kelman et al. 1989).

The use of aerial rather than subterranean tubers as seed for potatoes was proposed because comparable yields were obtained, and their higher concentration of Mg, glycoalkaloids, and chlorogenic acid were correlated with slower fungal growth, sporulation and infection (Percival et al. 1999). It is common to observe the accumulation of Si, Mg, Ca, P, S, Cl, and K in infection courts of *Erysiphe pisi* on susceptible peas (*Pisum sativum*). An inverse relationship was reported between chocolate spot (caused by *Botrytis fabae*) on *Vicia faba* and tissue Ca, Mg, and Zn (Rabie 1998). The concentration of Mg in potato periderm tissue, in contrast to Ca and P, was not correlated with susceptibility to common scab caused by *Streptomyces scabies* (Kristufek et al. 2000).

The correlation of disease conduciveness or suppressiveness of soils has been studied relative to Mg content. Clubroot suppressive soils are 3–15 times higher in Ca and Mg than clubroot conducive soils (Young et al. 1991). Biological control of take-all of cereals caused by the soilborne fungus *G. graminis* var. *tritici* by *Trichoderma koningii*, a Mn reducing soil fungus, was correlated with high levels of soil Mg although there was no correlation of Mg with soil conduciveness or suppressiveness of this disease (Duffy et al. 1997). Sugar maple decline was associated with low Mg, high Mn, and insect defoliation (Horsley et al. 2000). Although there was no direct effect of Mg in *Aphanomyces*-suppressive soils, as the level of Mg decreased, Ca and soil suppressiveness increased (Persson and Olsson 2000). Low soil availability of Mg and Ca with decreasing soil pH were associated with predisposition of cherry seedlings to infection by *Pseudomonas syringae* pv. *syringae* (Melakeberhan et al. 2000). In contrast, resistance of rice to panicle blast was positively correlated with tissue N, P, and Mg, and negatively correlated with tissue K and Ca which are decreased by Mg (Filippi and Prabhu 1998).

Magnesium, as well as Ca, is a critical nutrient for efficient N fixation by *Rhizobia.* A deficiency of Mg results in greatly reduced N fixation, although the high requirement for divalent cations can be met by either Ca or Mg (Vincent 1962). Soil Mg was not correlated with susceptibility of lodgepole pine to *Armillaria ostayae* (Mallett and Maynard 1998) or pears to fire blight (Koseoglu et al. 1996). Genetically engineered cotton, soybean, and corn plants for herbicide tolerance are typically lower in Mg and Mn and more susceptible to various diseases (Huber 2010; Johal and Huber 2009). The incidence of blight in pear trees was not affected by Mg directly, but the disease increased with N and decreased with K and Mn fertilization (Koseoglu et al. 1996) that interact with Mg.

Specific interactions of Mg with plant disease

Direct effects of Mg on disease are generally expressed when going from nutrient deficiency to sufficiency. Magnesium deficiency greatly increased infection and severity of peanut leaf spot caused by *Mycosphaerella arachidicola*, with the initiation of this disease manifest in leaves that show Mg deficiency first (Bledsoe et al. 1945). Although general pathways also may be involved, Mg can act more specifically in a particular host–pathogen interaction such as modifying symptom expression as observed with alfalfa mosaic virus (AMV) infection of common bean (*Phaseolus vulgaris*) where both Ca and Mg increase local lesion formation by AMV rather than systemic infection (Tu 1978) or increased resistance to extracellular pectin degrading enzymes of soilborne fungi and soft rot bacteria (Pagel and Heitfus 1990). Magnesium is a constituent of the middle lamella that, along with Ca, makes this pectic substance more resistant to degradation by pectolytic enzymes of various bacteria and fungal pathogens, and is a factor in the generally greater resistance of older tissues to macerating pathogens (Bateman 1964; Bonner 1950).

Several *Erwinia* species (*E. carotovora* subsp. *atroseptica*, *E. carotovora* subsp. *carotovora*, and *E. chrysanthemi*) cause soft rots of potato (*Solanum tuberosum*) and other plants by producing cell wall-degrading enzymes (Kelman et al. 1989; Pagel and Heitfus 1990). Plant resistance to these pathogens is related to the composition of the pectate substances in the middle lamella and degree of cross linkage with Ca or Mg (Pagel and Heitfus 1990).

Highest resistance to macerating enzymes of *Rhizoctonia solani* is observed in plants with the most Ca and Mg, and increased susceptibility of soybeans grown with low Ca and Mg is attributed to the thin walls of the cells (Kernkamp et al. 1952). The accumulation of multivalent cations such as Ca and Mg around infections of *R. solani* on hypocotyls of bean (*Phaseolus vulgaris*) leads to the development of pectates resistant to degradation by polygalacturonase and limited lesion development (Bateman 1964; Wood 1967). Since a single factor alone rarely confers resistance (Bateman 1978) the accumulation of these minerals around infection sites can serve as the activators, regulators, and inhibitors of the active physiologic mechanisms involved in plant defense (Huber 1980). Potato tissue with high Mg had increased resistance to gangrene caused by *Phoma exigua* (Kelman et al. 1989; McGuire and Kelman 1986) but decreased Ca content and lower resistance to bacterial soft rot caused by *Erwinia* spp. (McGuire and Kelman 1984; Pagel and Heitfus 1990). Early blight (*Alternaria solani*) of potato was significantly reduced with foliar applied Mg to provide a K:Mg ratio <3:1. A deficiency of Mg leads to early maturation and increased susceptibility to *Alternaria* (Elfrich 2010).

Examples of magnesium–disease interactions

Take-all of wheat

A sufficiency of Mg, like other nutrients, has been shown to be important in resistance of wheat to take-all caused by *Gaeumannomyces graminis* var *tritici* (Huber 1989a, b). The application of $MgCl_2$ to Mg-deficient soils, along with ammoniacal fertilizers that increase Mn availability, can reduce take-all and increase yields (Huber 1981). In contrast, the application of $MgCO_3$ as dolomitic lime ($CaCO_3$ + $MgCO_3$) to neutralize soil acidity and increase Mg availability also reduces the availability of Mn (Huber and McCay-Buis 1993) and can increase the severity of take-all of wheat and other cereals (Table 1). Magnesium is required by *Gaeumannomyces* for pathogenesis so that the depletion of Mg from soils with continuous cereal cropping or the use of ammonium sulfate fertilizers may be an important factor in the natural decline of take-all in the field (take-all decline, TAD). An alternative explanation could be the inhibition of nitrification by chloride and rhizosphere acidification to enhance mobilization of Mn (Huber and McCay-Buis 1993; Christensen et al. 1981). Avenacin produced in root exudates by oat varieties resistant to take-all inhibits Mg utilization by *G. graminis* var *tritici*, and ammonium or high levels of KCl also inhibit the uptake of Mg and reduce take-all (Huber 1989a, b; Jones and Huber 2007).

Bacterial spot of pepper and tomato

High levels of Mg significantly increased the development of bacterial spot of pepper and tomato caused by *Xanthomonas campestris* pv. *vesicatoria* (Woltz and Jones 1979). Bacterial spot was consistently 4 to 5 times less severe on both tomato and pepper when Mg was at the lower part of the normal range of Mg nutrition (0.44 %) than when it was at the higher end of the range (0.86 %) (Fig. 2). Bacterial spot was increased by either foliar applied $MgSO_4$ or soil applications of $MgCO_3$ in dolomitic lime (0.8 % tissue Mg) compared with the unamended control or soil-applied lime as $CaCO_3$ (0.5 % tissue Mg) (Fig. 3) (Jones et al. 1983) indicating that the increase with $MgCO_3$ wasn't necessarily because of a pH inhibition of Mn or K uptake but probably a more direct effect of Mg on the uptake of Ca or other minerals (James et al. 1995). A more direct effect of Mg to make the plant's physiology more conducive for the bacterial pathogen (Nayudu and Walker 1961) was indicated by the close correlation of tissue Mg with the percent bacterial spot in pepper (Fig. 4). Tissue levels of Mg were almost twice as high in plants grown in soil amended with dolomitic lime compared with only $CaCO_3$, and was highest when Mg was applied both to the soil and to foliage.

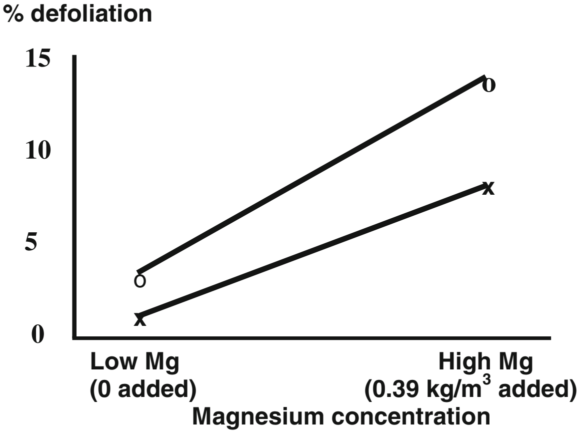


Fig. 2 Effect of magnesium concentration on defoliation of pepper (*x*) and tomato (*o*) plants by *Xanthomonas campestris* pv. *vesicatoria* (adapted from Woltz and Jones 1979)

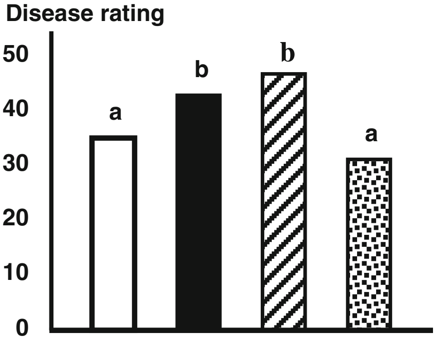


Fig. 3 Increased bacterial spot of pepper (*Xanthomonas vesicatoria*) with foliar- or soil-applied magnesium but not calcium (after Jones et al. 1983). Unamended control □, foliar Mg ■, soil Mg (dolomite lime) ▨, soil $CaCO_3$ ▩. *Bars with the same letter* are not significantly different

Inhibition of Mg uptake by K and N fertilization reduced leaf tissue concentrations of Mg and the development of bacterial spot in tomato caused by *X. campestris* pv *vesicatoria* (J.B. Jones et al. 1988). There was an inverse relationship between disease severity and Mg tissue concentration. As the N rate increased, Mg concentration and disease severity decreased. A similar effect of reduced severity of bacterial speck of Arabidopsis and tomato caused by

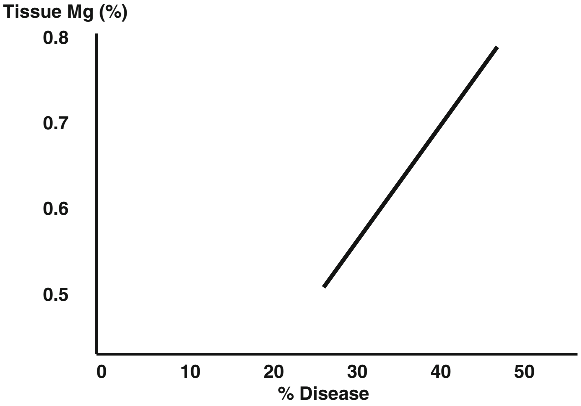


Fig. 4 Correlation of % bacterial spot of pepper (*X. vesicatoria*) with % tissue magnesium (after Jones et al. 1983)

Pseudomonas syringae pv *tomato*, by soil amendment with composted paper mill residues (PMRC) was associated with reduced foliar P. K, and Mg and the induction of plant defenses to this pathogen. There was no significant affect of composting PMR on tissue composition of other mineral elements (Vallad et al. 2003). In contrast, epiphytic populations of *X. campestris* pv. *vesicatoria* increased throughout each season concurrently with a decrease in soil Mg (McGuire et al. 1991).

Fusarium wilt of tomato

The uptake of K, Ca, and Mg of *Fusarium*-infected cotton plants is reduced (Sharoubeem et al. 1967) as a result of impaired vascular function (Huber 1978). High rates of lime were reported to reduce Fusarium wilt of tomato caused by *Fusarium oxysporum* f.sp. *lycopersici* as early as 1913 and has been confirmed for numerous crops since then (Jones et al. 1989). It was initially thought that liming increased Ca in tissues and inhibited polygalacturonase produced by the pathogen; however, only those nutrient sources that increased soil pH ($Ca(OH)_2$, $CaCO_3$, $CaCO_3$ +$MgCO_3$) reduced Fusarium wilt even though tissue Ca was similar with gypsum ($CaSO_4$) that didn't affect pH. NaCl, $FeCl_3$ and $MgCl_2$ increased wilt and may counteract the benefit of elements that increase pH in controlling wilt (Jones and Huber 2007) by inhibiting nitrification and increasing rhizosphere acidity (Christensen et al. 1981). Thus, the anion applied with the Mg appears to be the influential factor with this disease rather than the Mg cation and may be through its effect on cellular osmotic regulation (Elmer 2007) or soil acidification and increased availability of Mn (Huber and McCay-Buis 1993).

Liming soil to increase soil pH to 7.0–7.5 greatly limits the availability of micronutrients and consistently decreased wilt in naturally low pH soils. Chloride salts increase the availability of Fe, Mn, and Zn and offset the benefits of liming to achieve high soil pH. When soils of high soil pH suppressive to Fusarium wilt are amended with lignosulfonate metal complexes of Fe, Mn, or Zn to maintain plant availability of these micronutrients in high pH soils, the beneficial effects of high soil pH are reversed (Jones and Woltz 1970). Thus, the effect of high soil pH induced by liming limits the availability of micronutrients essential for the growth, sporulation, and virulence of the wilt fusaria rather than through increasing the availability of Ca or Mg and increased plant tissue resistance to maceration (Jones et al. 1989).

Soft rot of potato

Bacterial soft rots caused by *Erwinia* spp. frequently cause serious losses of potato both before and after harvest since there are no resistant varieties or chemical controls (Kelman et al. 1989). Infiltration of potato tubers with divalent cations (Sr, Mg, Ca) in general significantly reduced decay, with Ca being the most effective (Kelman et al. 1989; McGuire and Kelman 1986). Since only very high concentrations of Ca adversely affect growth of *Erwinia*, reduced decay has been considered primarily from increased resistance to tissue maceration (Kelman et al. 1989); however, pectic enzymes are important virulence factors for cell wall degrading, soft rotting *Erwinia* spp. (Collmer and Keen 1986). Polygalacturonase activity of *Erwinia* spp. was inhibited by divalent cations (Ca, Ba, Mg) while pectate lyase was enhanced by Ca, but not by Mg and Ba (Fig. 5) (McGuire and Kelman 1986; Pagel and Heitfus 1990; Perombelon and Kelman 1980). Pectinmethylesterase activity was generally not affected by either Ca or Mg (Pagel and Heitfus 1990).

Huanglongbing (greening disease, HLB) of citrus

HLB is a highly destructive disease of citrus caused by the phloem-limited *Candidatus* Liberibacter spp. of

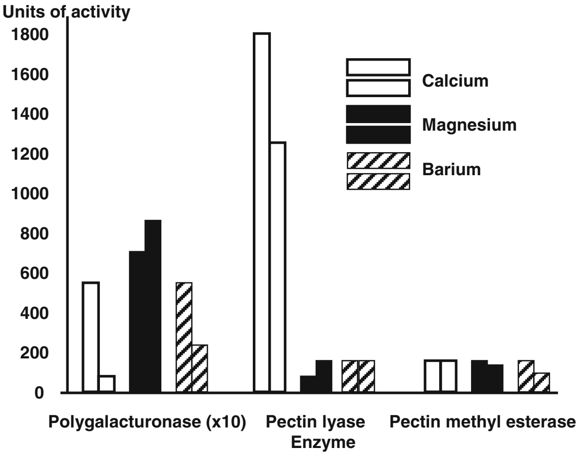


Fig. 5 Effect of divalent cations on pectic enzymes of *E. carotovora* subsp. *atroseptica* involved in tissue maceration (after Pagel and Heitfus 1990). The *bar to the left of each cation* is 1 mM and the *bar to the right* is 5 mM concentration

bacteria. This pathogen disrupts phloem transport to cause sugar and starch accumulation in leaves (source tissues), high sap proline concentrations, and Mn, Zn, and sink deficiency of carbohydrates (energy) leading to tree die-back and death (Timmer et al. 2000). Genetic resistance and chemical controls of this disease are not known so that control in infected trees has only been achieved by changing the plant environment and physiological functions that favor restored mineral mobility and sugar transport in phloem tissues, mineral sufficiency and insect vector control. Magnesium and K are used to enhance phloem movement of photosynthates, Mn, Zn, B, and other mineral elements are optimized through foliar application with phosphorus acid or as phosphonates along with a strong supporting soil nutrient program (Rouse et al. 2012). Productivity and fruit quality has been maintained or improved by integrating critical mineral nutrition with best management practices in spite of nearly 100 % tree infection as described earlier.

Conclusions

The relationship of Mg to disease has been determined from direct response to Mg amendment, comparison of Mg in tissues of diseased and non-diseased plants, comparison of disease conducive and suppressive soils, and differences in populations of pathogens in high- and low-Mg environments (Jones and Huber 2007). Magnesium nutrition may increase some diseases such as bacterial spot of tomato and pepper and reduce other diseases, such as bacterial soft rot of tomato. Similar effects with some diseases are obtained regardless of the Mg source and whether supplied through the roots (soil) or foliage; while specific salts of Mg can have different effects with other diseases. The rate, source, time of application, nutrient status of the plant, and interactions with other minerals in the plant or pathogen are important considerations in understanding the role of Mg in disease resistance or susceptibility. A specific mechanism of defense to diseases enhanced by Mg includes increased resistance of tissues to degradation by pectolytic enzymes of bacterial soft rotting pathogens. Increased susceptibility to other diseases may be through competition for Ca uptake and reduced resistance of these tissues to degradation. Reduced virulence of pathogens at the higher pH provided by dolomitic lime ($CaCO_3 + MgCO_3$) appears to be from the reduced availability of essential micronutrients. Management of Mg nutrition in balance with other minerals to reduce disease is an underutilized tool for disease control.

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