

Managing Nutrition to Control Plant Disease.

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Introduction

Plant diseases are a major limitation to improved production efficiency and crop quality as they reduce nutrient availability, uptake, distribution, or utilization by the plant. Disease symptoms frequently reflect the altered nutritional status of the plant and it is frequently difficult to clearly distinguish between the biotic and abiotic factors involved. Immobilization of Mn at the infection site by *Gaeumannomyces graminis* var *tritici* or *Magnaporthe grisea* predisposes wheat tissues to take-all or rice to blast, respectively. The ability to oxidize Mn from the reduced, plant available form, to the oxidized, non-available form, is a virulence mechanism of pathogens, and isolates of *G. graminis* and *M. grisea* that can not oxidize Mn are also avirulent (Huber and Thompson, 2006). Nutrients accumulating around infection sites are unavailable to the plant as are those that accumulate in hyperplasias induced by certain bacteria, fungi, and nematodes. Restricted root growth from necrosis, girdling, or acropital infection can directly affect nutrient absorption and predispose plants to more severe infection or to other pathogens. A malfunctioning vascular system or changes in membrane permeability can induce a systemic or localized nutrient deficiency. Increased permeability can result in the loss of nutrients through root or leaf exudation to attract pathogens or enhance infection. This phenomenon is common with a deficiency of Zn or B where infection by zoosporic organisms is enhanced by deficiency.

The availability of genetic resistance to disease has permitted the production of many crops in areas that would otherwise be non-profitable because of certain diseases; however, providing nutrient sufficiency continues as a primary component for the full expression of genetic resistance, and the only control available for many common diseases for which genetic resistance is not available. Many cultural disease control tactics such as crop sequence, organic amendment, soil pH adjustment, tillage, and irrigation management frequently influence disease through nutrient interactions. These practices supply nutrients directly or make them more available to a plant through altered biological activity. As management practices such as the move to non-tillage or single source herbicide occur that influence plant nutrients, old diseases have increased and new ones appear. The availability of inorganic fertilizers has brought about the demise of many diseases through improved plant resistance, disease escape, or altered pathogenicity. Some general references on nutrient-disease interactions include Datnoff et al. (2006), Engelhard (1989), Graham (1983), Graham and Webb (1991), Huber (1978, 1980), Huber and Graham (1999), and Huber and Watson (1974).

Nutrition influences all of the interacting components affecting disease severity (Fig. 1). As part of the “environment,” nutrients influence plant, pathogen, and microbial growth to remain an important factor in disease control. The interaction of nutrition in these components is dynamic and all essential nutrients are reported to influence the incidence or severity of some diseases. A particular element may decrease the severity of some diseases, but increase others, and some have an opposite effect in different environments. Some forms of biological disease control and ‘suppressive soils’ are manifestations of microbial activity that influence nutrient

availability (Huber, 1989; Huber and Graham 1999). In general, the greatest benefit to the plant is provided when full nutrient sufficiency is provided; however, the response to a particular nutrient may be different when going from deficiency to sufficiency than from sufficiency to excess. Since each nutrient functions as part of a delicately balanced interdependent system with the plants genetics and the environment, it is important to establish a nutrient balance for optimum crop response. Through an understanding of the disease interactions with each specific nutrient, the effects on the plant, pathogen, and environment can be effectively modified to improve disease control, enhance production efficiency, and increase crop quality.

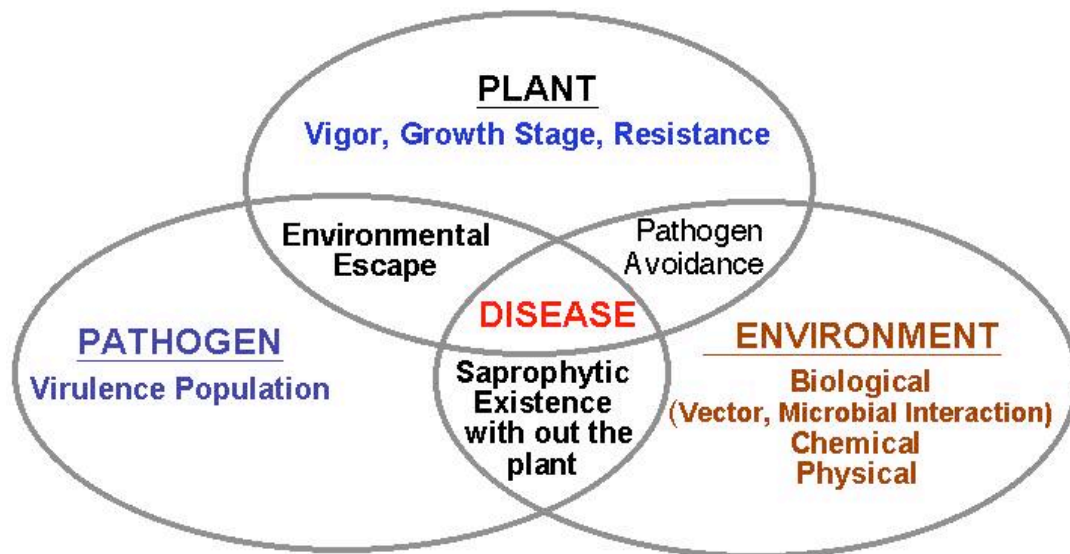


Figure 1. A schematic representation of the interacting components involved in plant disease.

Correlating nutrient effects with disease.

The association of mineral nutrition with disease has been based on 1) the observed effects of fertilization on a specific disease's incidence or severity, 2) the comparison of mineral concentrations in healthy or resistant tissues compared with diseased or susceptible tissues, or 3) conditions influencing the availability of a specific nutrient with disease. All of these observations can generally be correlated for a particular nutrient and disease interaction although plant stage of growth, environmental conditions, and biological activity can all influence the outcome.

The effect of many nutrients on disease has been observed incidentally as a consequence of fertilizing to optimize plant growth or yield, and then confirming the observations under more

controlled conditions in the greenhouse or field. The use of inorganic mineral fertilizers permits a direct observation of a nutrient's effects that could only be generalized when organic manuring or crop rotation was studied, but should not exclude consideration of the role of soil organisms in the process. A standard recommendation to maintain optimum N fertilization to decrease take-all of cereals derives from early observations that N deficiency predisposed plants to take-all. It is now known that a deficiency of most essential nutrients will increase severity of this disease. Barnyard manure high in zinc from animal rations that is applied prior to planting winter wheat greatly reduces the severity of spring blight caused by *Rhizoctonia cerealis* similar to providing preplant Zn (Fig. 2). Copper deficiency causes male sterility in gramineous crops, and wheat deficient in Cu is predisposed to ergot as the florets open for cross-pollination. Providing a sufficiency of Cu for wheat nutrition greatly reduces ergot severity and increases wheat yield (Table 1). Resistance of wheat and flax to rust, and maize to Stewart's wilt, may be lost under K-deficient conditions (Huber and Arny, 1985).

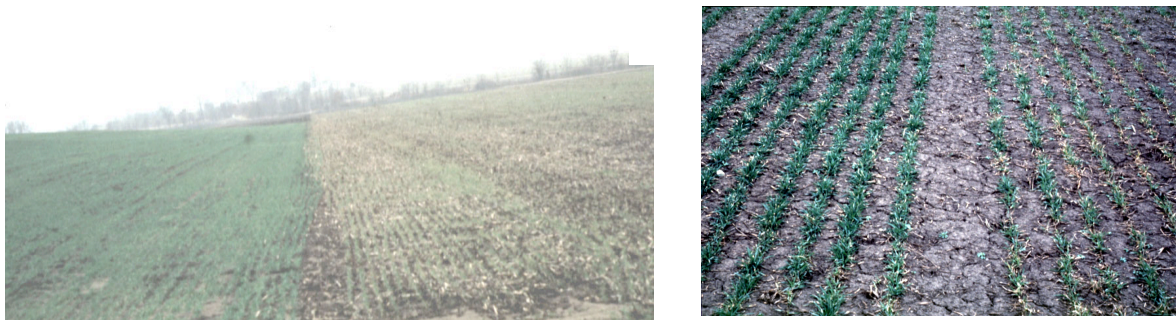


Figure 2. Effect of preplant-applied Zn on spring blight of wheat. A) Fall-applied barnyard manure high in Zn (left) compared with non-manured wheat (right). B) Preplant-applied Zn (left) compared with non-Zn fertilized wheat (right).

Table 1. Effect of copper on ergot severity in wheat (after Evans et al., 2006).

Treatment	Grain yield (kg/ha)	Ergot sclerotia per acre
Non-fertilized	362	17,743
10 kg/ha Cu	1,144	2,420

The correlation of tissue nutrients in diseased compared with healthy, or susceptible compared with resistant, plants has also provided insight into nutrient-disease interactions and specific examples are reported for most of the essential nutrients. Resistance of rice to blast, sheath blight, brown spot and stem rot is correlated with high Si content in plant tissues (Savant et al., 1997). High Ca in tissues is correlated with resistance to macerating diseases caused by *Erwinia carotovora*, *Fusarium solani*, *Pythium myriotylum*, *Rhizoctonia solani*, *Sclerotinia minor*, and *Sclerotium rolfsii* (Bateman and Basham, 1976, Kelman et al., 1989, and Huber, 1994). Wilt resistant flax takes up more K than susceptible varieties (Sharville, 1936). Zinc was

higher in tissues of wheat where *R. cerealis* was less severe compared with areas where spring blight was more severe (Table 2).

Table 2. Concentration of Zn in wheat tissues correlated with severity of spring blight (after Huber and Graham, 1999).

Treatment	Tissue Zn		Plants killed	
	Without ^a	With	Without ^a	With
	mg/kg ⁻¹		%	
Barnyard manure	20	41	80	18
Sediment area of field	17	27	100	45
Tree leaf-drop area	19	34	65	20

^aWithout the treatment or outside the area of influence

Correlation of conditions that influence the availability of various nutrients have led to the general grouping of diseases as high or low pH, moisture, or specific nutrient diseases (Huber and Graham, 1999). The effect of specific crop rotations or sequences and their residues on nitrification was consistent with the effect of the form of nitrogen on specific diseases (Huber and Watson, 1974). Many cultural disease control practices function through their effect on mineral nutrient availability (Table 3). The transformation from insoluble Mn⁺³ or Mn⁺⁴ oxides to plant-available soluble Mn⁺² is highly dependent on environmental factors so that many of the factors that predispose plants to disease do so through their influence on Mn availability. The greater resistance of paddy-grown rice to blast (*Magnaporthe grisea*) compared with upland rice has been attributed to the greater uptake of Mn under paddy conditions (Pearson and Jacobs, 1986).

Table 3. Correlation of factors affecting nitrification and Mn availability with disease severity.

Factor	Nitrification	Mn availability	Disease severity ^a
Low soil pH	Decrease	Increase	Decrease
Green manures (some)	Decrease	Increase	Decrease
Ammonium fertilizers	Decrease	Increase	Decrease
Irrigation (some)	Decrease	Increase	Decrease
Firm seed bed	Decrease	Increase	Decrease
Nitrification inhibitors	Decrease	Increase	Decrease
Soil fumigation	Decrease	Increase	Decrease
Metal sulfides	Decrease	Increase	Decrease
Glyphosate	Increase	Decrease	Increase
High soil pH	Increase	Decrease	Increase
Application of lime	Increase	Decrease	Increase
Nitrate fertilizers	Increase	Decrease	Increase
Manure	Increase	Decrease	Increase
Low soil moisture	Increase	Decrease	Increase
Loose seed bed	Increase	Decrease	Increase

^aPotato scab, rice blast, wheat take-all, corn stalk rot, Phymatotrichum root rot.

Managing nutrition to control disease.

Manipulating the various interactions of the plant, pathogen, and environment over time can reduce most diseases. Considerations include 1) the level of genetic resistance of the plant (highly susceptible, tolerant, resistant, or immune) and nutrient availability relative to plant needs (deficiency, sufficiency, excess), 2) the predominant form and biological stability of a nutrient that is applied or available (oxidized or reduced), 3) the rate, time and method of nutrient application, 4) nutrient balance and associated ions, and 5) integration of fertilization with other crop production practices.

Genetic resistance and nutrient sufficiency. Cultivars that are tolerant or resistant to disease are generally more responsive to nutrient manipulation than highly susceptible cultivars, while cultivars that are immune to a particular disease such as rye to take-all, may be highly efficient in nutrient uptake. In contrast to rye, wheat is inefficient in micronutrient uptake and highly susceptible to take-all (Figure 4). Maize hybrids resistant to Diplodia and Gibberella stalk rots are efficient in N uptake and do not cannibalize the Rubisco and Pep Carboxylase enzymes important in photosynthesis as N sources for developing kernels (Huber et al., 1986). Take-all and tan spot of wheat and stalk rot of corn decrease in severity as N increases from deficiency to physiological sufficiency. Excess N may decrease resistance to stalk rot because the physiological sufficiency of other nutrients may not be in balance (Warren et al., 1980) or pathogen activity is enhanced (Graham and Webb, 1991).

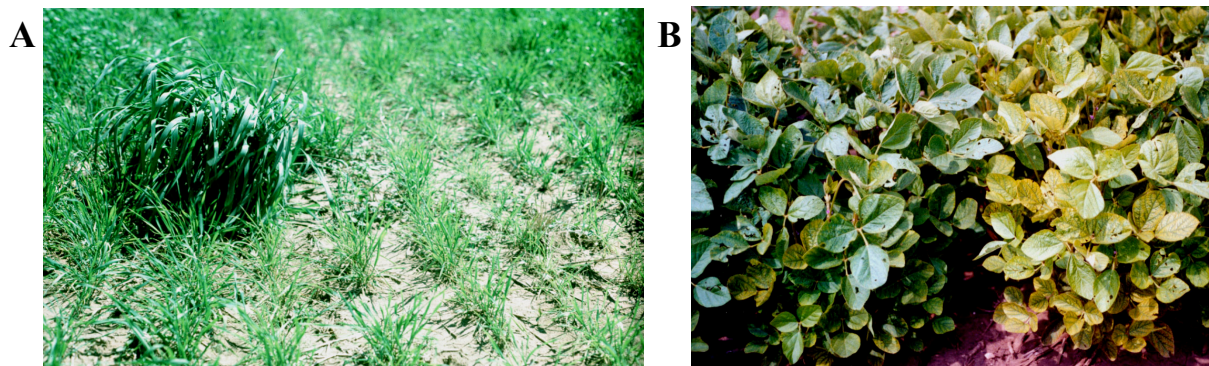


Figure 4. Differences A) in growth and take-all of Mn-efficient rye (green, vigorous plants) compared with stunted inefficient wheat in a low Mn soil, and B) a Mn efficient (left) and Mn inefficient (right) soybean varieties growing in a low Mn soil.

The predominant form and biological stability of a nutrient. Different forms of a nutrient often influence disease differently because of differences in plant uptake or physiological pathways involving specific defense mechanisms. Elements such as N, Fe, Mn, and S are readily oxidized or reduced in most soils by soil microorganisms to affect their availability for plant

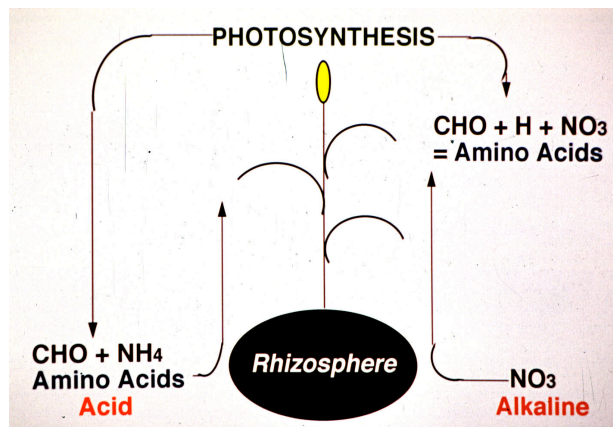
uptake. Microbial Mn oxidation is so rapid in most cultivated soils that Mn soil amendments are seldom efficient in overcoming Mn deficiency. Reducing conditions favored in an anhydrous ammonium fertilizer band applied to corn are frequently observed as increased Mn availability for a subsequent soybean crop in low Mn soils. Oxidizing conditions predominate when nitrate is the source of N fertilizer and can be used with Ca to reduce Mn toxicity in high Mn environments.

The biological mineralization of organic N to ammonium and its subsequent nitrification to nitrate are dynamic processes that provide a preponderance of one or the other forms of N for plant uptake depending on the soil environment and biological activity. Both the cationic (NH_4^+) and anionic (NO_3^-) forms of N are assimilated by plants, but they may have opposite effects on disease (Huber and Watson, 1974) because they are metabolized differently (Fig. 5). Diseases such as Verticillium wilt, take-all, Streptomyces scab, and rice blast that are reduced by ammonium are also reduced by environmental conditions that slow or inhibit nitrification and increase the availability of Mn. In contrast, diseases reduced by nitrate are also less severe with Ca and environmental conditions that favor nitrification so that practical control of some diseases can be obtained by manipulating the environment to favor one or the other forms of N. Clubroot, Rhizoctonia canker and Fusarium wilts of fruit and vegetable crops can be controlled by liming to increase soil pH and fertilizing with a nitrate source of N (Huber, 1989; Jones et al., 1989). These diseases also are less severe following crops that enhance nitrification (Huber and Graham, 1999).

Crop removal of residual nitrates or inhibiting nitrification may be required to benefit from ammonium nutrition. Inhibiting nitrification of ammonium fertilizers with CS_2 , K_2S , P_2S_5 or nitrapyrin have provided effective control of potato scab caused by *Streptomyces scabies* when residual nitrates are reduced (Huber and Watson, 1974). Soil fumigation with dichloropropane, methyl bromide, or chloropicrin inhibits nitrification and has been extensively used to control Verticillium wilt and other diseases of high-value crops. The benefits of fumigation for Verticillium wilt control can be enhanced with ammonium and reduced by nitrate sources of N (Huber and Graham, 1989). Inhibiting nitrification of animal manures removes their predisposition of corn to stalk rot and reduces leaching and denitrification losses to increase N efficiency and grain yield.

The rate, time and method of nutrient application. Mineral nutrients are applied to meet the potential needs for efficient crop production in an economically and environmentally sound manner. The greatest disease responses are observed when going from deficiency to plant sufficiency; however, the needs and uptake of nutrients depend on the stage of plant growth, availability of nutrients in the soil, time of application, microbial activity, and general health of the plant. The time of fertilization is important to minimize periods of irreversible nutrient deficiency without stimulating pathogenic activity. Fall application of N stabilized with a nitrification inhibitor for winter wheat in the Pacific Northwest (USA) provided full sufficiency of N throughout the crop season without affecting eyespot (*Pseudocercospora herpotrichoides*), while disease severity increased with increasing rates of spring-applied N to decrease yield as N rates approached full sufficiency (Figure 6). Rhizoctonia spring blight (*R. cerealis*) and sharp eyespot of winter wheat is increased when N is applied during the cool, wet period when the wheat is dormant and the environment conducive for this disease, but is not

affected under less conducive environmental conditions in the fall or late spring. Liquid N increases spring blight more than granular fertilizers because of enhanced contact with the pathogen and increased production of pathogenesis required macerating enzymes (Table 4).



Infection	kg N/ha	Grain yield	% Infection	kg N/ha	Grain yield	% Infection
0	0	3000	0	0	3000	0
0	55	5250	20	55	6000	20
0	110	4500	40	110	5250	40
0	165	3750	60	165	4500	60
0	3000	3000	80	3000	3000	80
	kg N/ha Fall-applied			kg N/ha Spring-applied		

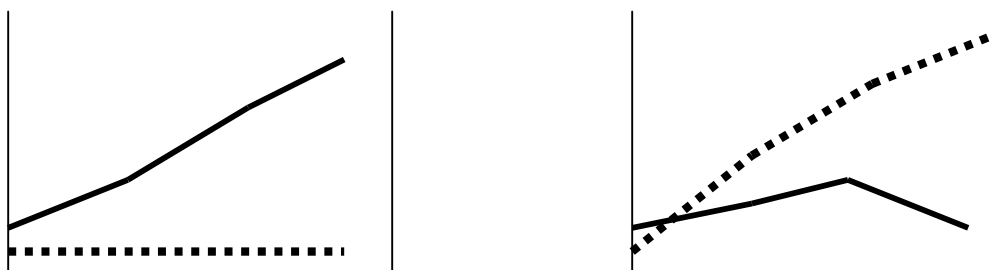


Figure 6. Effect of time and rate of N fertilization on wheat yield and eyespot infection. Solid line is grain yield; dashed line is % infection (after Huber, 1989).

Table 4. Effect of N source and time on Rhizoctonia spring blight of winter wheat (after Huber and Graham, 1999).

N source	Time applied	Percent of plants killed
Anhydrous ammonia + NI*	September	14
Urea granules	February	40
28% N solution	February	60
Urea granules	April	14

* Nitrapyrin as a nitrification inhibitor

Nutrient balance and associated ions. Nutrient imbalance may be as detrimental to plant growth and disease resistance as a deficiency. Potassium decreases take-all of wheat if N and P are sufficient, but increases this disease if they are deficient. Fusarium wilt of tomato and yellows of cabbage, Stewart's wilt of corn, and downy mildew of tobacco are increased by K if there is an imbalance of other nutrient elements (Huber and Arny, 1985). Fusarium wilt of cotton, Streptomyces scab of potato, clubroot of crucifers and late blight of potato have been correlated with the ratio of K to Mg, Ca, and N, respectively, rather than the actual amount of either element individually (Huber, 1980).

The associated ion applied with an organic or inorganic fertilizer salt may have an effect on disease independent of the primary ion. As previously mentioned, Zn in barnyard manure was the key to reduced Rhizoctonia spring blight rather than the N, P, or K that were also available. Stalk rot of corn, take-all of cereals, northern corn leaf blight, and rusts on wheat are reduced by high rates of KCl, and similar effects are observed with NaCl and NH₄Cl, but not with K₂SO₄ or KH₂PO₄ (Huber and Arny, 1985). The Cl ion also has been shown to inhibit nitrification and increase Mn solubility and facilitate its chemical reduction.

The integration of fertilization with other crop production practices. Crop rotation and early fallowing practices increased the supply of readily available nutrients and controlled weeds that competed for nutrients and moisture. Both practices contributed to disease reduction and are still important practices to control soilborne diseases. Long-term monoculture of cereals leads to the biological reduction of take-all through a phenomenon referred to as take-all decline that is associated with an increase in Mn availability (Huber and McCay-Buis, 1993). Corn provided almost twice the available Mn for a subsequent crop than wheat or soybeans in long-term crop sequence studies (Smith, 2006). Oats produce glycosyanide root exudates that are toxic to Mn-oxidizing rhizosphere organisms and provide excellent control of take-all for a subsequent wheat crop; however, rye, resistant to take-all, as a precrop to wheat has no effect on take-all of a subsequent wheat crop (Rothrock and Cunfer, 1991).

Tillage, seeding rate, and pH adjustment accentuate the benefits of nutrient amendment by modifying the environment for plant growth, nutrient access, or microbial activity. A firm seed bed, long recommended to reduce the severity of take-all, increases Mn uptake by wheat. In contrast, take-all of wheat, Corynespora root rot of soybean, and Fusarium head scab are more severe after application of the herbicide glyphosate, a strong metal chelator that is toxic to Mn reducing organisms (Fig. 7)) (Huber et al., 2005). Plant growth promoting rhizosphere bacteria

applied to seed or transplants reduce disease by modifying the microbial environment and increasing the availability of specific micronutrients such as Fe and Mn (Huber and McCay-Buis, 1993). Inhibiting nitrification of ammonium fertilizers prevents leaching and denitrification losses of N and increases the availability of Mn for control of take-all (Fig. 8). Nutrition should be used in conjunction with disease resistance, crop sequence, weed control, and insect management to optimize plant productivity.



Figure 7. Increased severity of take-all of wheat following the application of glyphosate herbicide (left) compared with wheat after another herbicide (right).



Figure 8. Reduced take-all of wheat fertilized with ammonium N stabilized with a nitrification inhibitor (right) compared with ammonia alone (left).

Mechanisms of disease control with nutrition

Passive and active mechanisms of disease control are activated through nutrient management. Mineral nutrients are the components of plants and regulate metabolic activity associated with resistance of a plant and virulence of a pathogen. Adequate nutrition is generally required to maintain a high level of disease resistance. Plants contain preformed anti-microbial compounds and have active response mechanisms where inhibitory phytoalexins, phenols, flavonoids, and other defense compounds accumulate around infection sites of resistant plants if the nutrients required for the synthesis or induction of those compounds are adequate. An adequate supply of Mn and several other micronutrients are important in most of the active defense mechanisms mediated through the Shikimate pathway. Glycoproteins (lectin) associated with resistance of sweet potato to *Ceratocystis fimbriata* (black rot) and potato to *Phytophthora infestans* (late blight) require Mn for activity (Garas and Kuc, 1981). Vascular concentrations of chlorogenic acid inhibitory to pectin methyl esterase of vascular *Verticillium* remains much higher in resistant than susceptible potato cultivars (Figure 9). Disease onset is observed in 90 to 100 days after planting of susceptible cultivars fertilized with nitrate and delayed until 120-140 days when these cultivars are fertilized with ammonium stabilized with a nitrification inhibitor (Huber and Watson, 1974).

Nutrients such as Ca that suppress macerating diseases caused by bacterial soft rots (*Erwinia*), *Sclerotium rolsii*, *Pythium myriotylum*, *Rhizoctonia solani*, *Cylindrocladium crotalariae*, *Sclerotinia minor*, and *Fusarium solani* increase the structural integrity and resistance of the middle lamella, cell wall components, and cell membranes to the extracellular macerating enzymes produced by these pathogens (Bateman and Basham, 1976; Kelman et al, 1989). Nitrate sources of N suppress production of these enzymes while ammonium may increase them (Huber and Graham, 1999). Magnesium is also important for structural integrity of cell components and also may reduce susceptibility to pathogen-produced macerating enzymes as long as Ca levels remain sufficient (Csinos and Bell, 1989). Silicon is combined with other components to give cell walls greater strength as physical barriers to penetration by *Pyricularia grisea* (rice blast) and *Erysiphe* spp. (mildews), and is involved in physiological responses to infection by increasing the availability of K and mobility of Mn (Datnoff et al, 1991 and Savant et al, 1997).

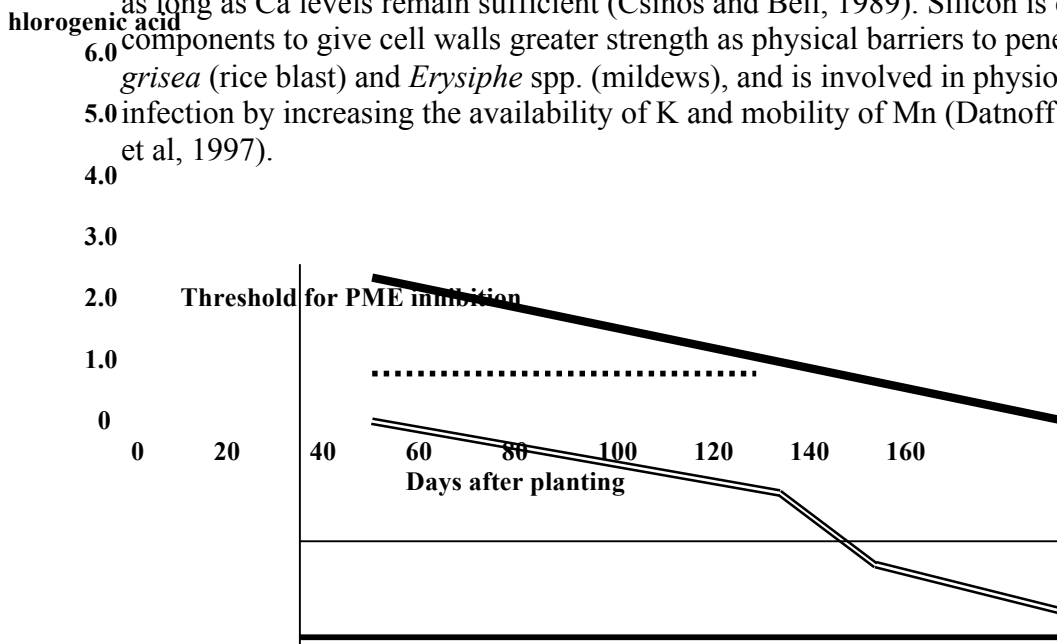


Figure 9. Concentration of vascular phenolic compounds (chlorogenic acid) inhibitory to pectin methyl esterase (PME) in *Verticillium* wilt susceptible and resistant potato varieties.
 — = Resistant P141256, = Early Gem, ===== = Russet Burbank (After Huber, 1989).

Nutrient sufficiency may provide a general form of disease resistance by maintaining a high level of inhibitory compounds in tissue or quick response to invasion by a pathogen. The rapid cicatrization around a wound or infection site that limits damage by an invading pathogen requires a sufficiency of Mn and other essential micronutrients (Graham, 1983; Huber and Graham, 1999). Differences in metabolism of different forms of a nutrient such as N may deny an obligate pathogen of essential intermediate compounds needed for survival, pathogenesis, or reproduction. Resistance of potato to *Phytophthora* is associated with the K-induced accumulation of fungistatic levels of arginine in leaves (Alten and Orth, 1941). Potassium reduces the high levels of glutamine and glutamic acid in tobacco plants susceptible to *Alternaria*, *Cercospora*, and *Sclerotinia* to make the plants less susceptible to these pathogens (Klein, 1957).

Providing adequate N throughout the grain fill period is important to minimize the cannibalization of physiological and structural proteins required for resistance that the plant will otherwise use to meet the N needs of developing kernels (Huber et al., 1986). Nutrient sufficiency also may shorten a susceptible growth stage for some plant-pathogen interactions. A response to fertilization by increased growth may constitute a form of disease escape. Phosphorus and N stimulate root growth of cereal plants so that P and N sufficient plants are able to compensate for tissue lost through root rots such as take-all and *Pythium* (Huber, 1980). Specific nutrients such as N and S may change the abiotic and biotic soil environment to favor specific nutrient uptake, biological control, or enhance genetic resistance.

Interaction of nutrients with the biological environment

Microbes in the environment may enhance or inhibit disease through their effect on nutrient availability. Manganese oxidation is a virulence factor for *Gaeumannomyces graminis*, *Magnaporthe grisea*, and *Streptomyces scabies* so that isolates that can't oxidize Mn are avirulent (Fig. 10). Oxidation immobilizes Mn and creates a localized deficiency so that resistance of the plant is compromised at the infection site (Thompson and Huber, 2006). *Magnaporthe grisea* produces two toxins (alpha-picolinic acid and piricularin) that are strong chelating agents and increase the mobility of Mn to the infection site where it is rapidly oxidized by the pathogen (Cheng et al., 2005). Rapid growth of microorganisms on freshly buried high carbon residues can immobilize nutrients in their cells and compete for nutrients needed for plant growth. This is a common phenomenon when large quantities of straw are incorporated in soil without additional N to hasten decomposition and compensate for microbial immobilization.

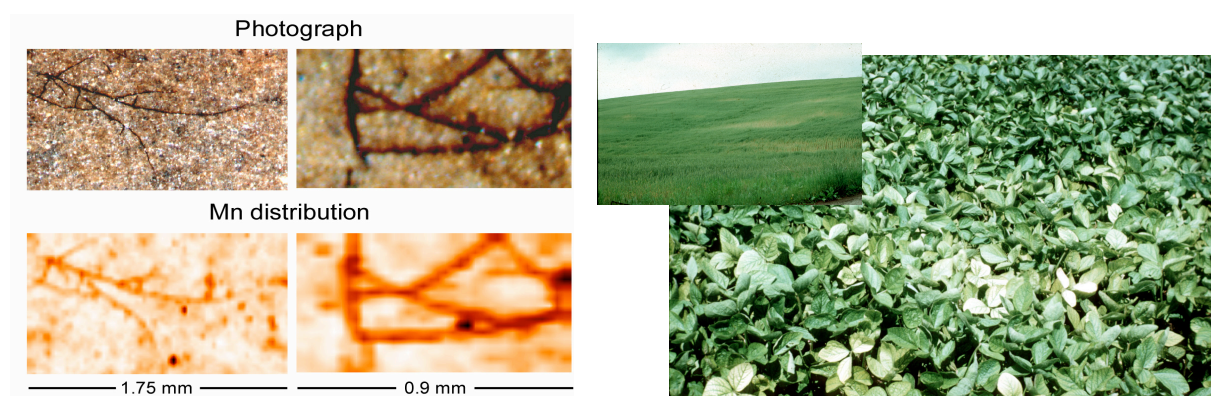


Figure 10. Manganese oxidation by a virulent isolate of *Gaeumannomyces graminis* in soil (upper left photograph of mycelial networks in soil; lower left are micro-x-ray XANES spectroscopy of Mn-oxide distribution showing the dark mycelial filaments associated with Mn oxidation) and biologically-induced Mn deficiency in soybeans double-cropped after severe take-all (insert) of wheat (Thompson and Huber, 2006).

Biological mineralization and oxidation-reduction activities of microorganisms are critical in maintaining nutrient availability for crop production. Mineralization converts organic complexes to soluble inorganic nutrients available for plant uptake. Although N can be absorbed by plants as either the reduced (ammonium) or oxidized (nitrate) form, other nutrients are

available to plants only in the reduced (Fe, Mn) or oxidized (S) form so that plant sufficiency may be more dependent on rhizosphere biological activity than the actual amount of an element in soil. Changes in soil biological activity can have a significant effect on disease because of subsequent changes in nutrient availability. Dung left by cattle in a wheat field stimulate Mn oxidizing organisms and increase take-all, and toxicity of glyphosate herbicide to Mn reducing organisms increases *Corynespora* root rot of soybean (Fig. 11). Seed bacterization of wheat with Mn-reducing organisms increases the availability of Mn and reduces take-all root rot (Huber and McCay-Buis, 1993).

Summary and conclusions

Nutrient management through amendment, improved genetic efficiency, and modification of the environment is an important cultural control for plant disease and an integral component of efficient production agriculture. Disease resistance is genetically controlled but mediated through physiological and biochemical processes interrelated with the nutritional status of the plant or pathogen. The nutritional status of a plant determines its histological or morphological structure and properties, and the function of tissues to hasten or slow penetration and pathogenesis. Pathogen virulence and their ability to survive are also conditioned by various nutrients; however, most nutrients influence disease potential more than inoculum potential. The intricate relationship of the plant's nutritional status with plant pathogens, the abiotic environment and organisms in the environment is dynamic and the severity of most diseases can be greatly decreased by proper nutrient management. Knowledge of the relationship of plant nutrition to disease provides a basis for reducing disease severity in intense as well as integrated crop production systems.

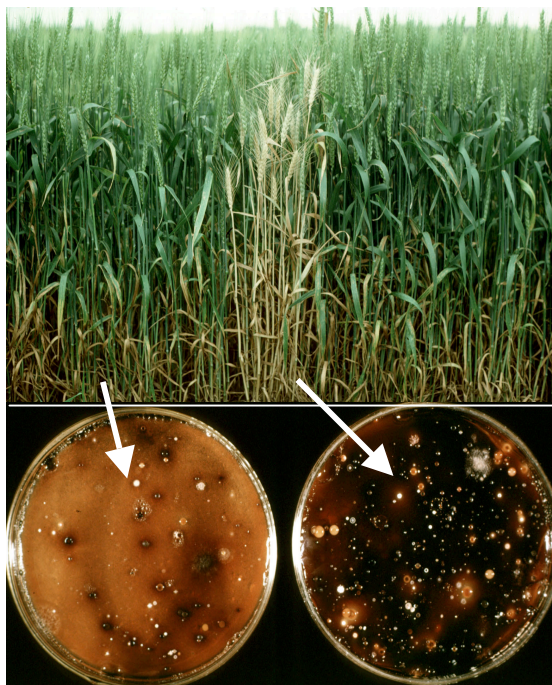


Figure 11. Severe take-all with dung (above center) compared with adjacent non-dunged wheat (left). High population of Mn-oxidizing

(dark colonies) organisms in the dunged wheat rhizosphere (right) compared with the non-dunged wheat (left).

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