

Role of Nutrients Availability in Fruit and Vegetable Disease Control

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ABSTRACT

In recent years, plant diseases play a major limiting role in agricultural production. The control of plant diseases using classical pesticides raises serious concerns about food safety, environmental quality and pesticide resistance, which have dictated the need for alternative pest Management techniques. In particular, nutrients could affect the disease tolerance or resistance of plants to pathogens. However, there are contradictory reports about the effect of nutrients on plant diseases and many factors that influence this response are not well understood. This Review article summarizes the most recent information regarding the effect of nutrients, such as N, K, P, Mn, Zn, B, Cl and Si, on disease resistance and tolerance and their use in agriculture. There is a difference in the response of obligate parasites to N supply, as when there is a high N level there is an increase in severity of the infection. In contrast, in facultative parasites at high N supply there is a decrease in the severity of the infection. K decreases the susceptibility of host plants up to the optimal level for growth and beyond this point there is no further increase in resistance. In contrast to K, the role of P in resistance is variable and seemingly inconsistent. Among the micronutrients, Mn can control a number of diseases as Mn has an important role in lignin biosynthesis, phenol biosynthesis, photosynthesis and several other functions. Zn was found to have a number of different effects as in some cases it decreased, in others increased, and in others had no effect on plant susceptibility to disease. B was found to reduce the severity of many diseases because of the function that B has on cell wall structure, plant membranes and plant metabolism. Cl application can enhance host plants' resistance to disease. Si has been shown to control a number of diseases and it is believed that Si creates a physical barrier which can restrict fungal hyphae penetration, or it may induce accumulation of antifungal compounds. Integrative plant nutrition is an essential component in agriculture, because in most cases it is more cost effective and also environmentally friendly to control plant disease with the adequate amount of nutrients and with no pesticides. Nutrients can reduce disease to an acceptable level, or at least to a level at which further control by other cultural practices or conventional organic biocides are more successful and less expensive.

Keywords: Disease resistance, Nutrients, Deficiency, Susceptibility, Metabolism

INTRODUCTION

Nutrients are important for growth and development of plants and also microorganisms, and they are important factors in disease control (Agrios, 2005). All the essential nutrients can

affect disease severity (Huber and Graham, 1999). However, there is no general rule, as a particular nutrient can decrease the severity of a disease but can also increase the severity of the disease incidence of other diseases or have a completely opposite effect in a different environment (Marschner, 1995; Graham and Webb 1991). Despite the fact that the importance of nutrients in disease control has been recognized for some of the most severe diseases, the correct management of nutrients in order to control disease in agriculture has received little attention (Huber and Graham, 1999). Nutrients can affect disease resistance or tolerance (Graham and Webb, 1991). Disease resistance of the host is its ability to limit the penetration, development and reproduction of the invading pathogens (Graham and Webb, 1991). On the other hand, tolerance of the host is measured in terms of its ability to maintain its own growth or yield in spite of the infection. Resistance depends on the genotype of the two organisms, plant age and changes in the environment. Although plant disease resistance and tolerance are genetically controlled (Agrios, 2005), they are affected by the environment and especially by nutrient deficiencies and toxicities (Marschner, 1995; Krauss, 1999). The physiological functions of plant nutrients are generally well understood, but there are still unanswered questions regarding the dynamic interaction between nutrients and the plant-pathogen system (Huber, 1996a). In addition, nutrients can affect the development of a disease by affecting plant physiology or by affecting pathogens, or both of them. The level of nutrients can influence the plant growth, which can affect the microclimate, therefore affecting infection and sporulation of the pathogen (Marschner, 1995). Also, the level of nutrients can affect the physiology and biochemistry and especially the integrity of the cell walls, membrane leakage and the chemical composition of the host, e.g. the concentration of phenolics can be affected by B deficiency (Graham and Webb, 1991).

NUTRITION AND DISEASE CONTROL AND ROLE OF NUTRIENTS IN REDUCING DISEASE SEVERITY

When a plant is infected by a pathogen its physiology is impaired and especially nutrient uptake, assimilation, translocation from the root to the shoot and also utilization (Marschner 1995). There are pathogens that can immobilize nutrients in the rhizosphere, the soil surrounding plant roots, or in infected tissues such as roots, while others interfere with translocation or utilization efficiency and can cause nutrient deficiency or hyper accumulation and nutrient toxicity (Huber and Graham, 1999). Also, other organisms can utilize a significant amount of nutrients for their growth, causing a reduction in the availability of nutrients for the plant and increasing its susceptibility due to nutrient deficiency. One of the most common symptoms of many soil borne pathogens is root infection, which reduces the ability of the root to provide the plant with water and nutrients (Huber and Graham, 1999). This effect is more serious when the levels of nutrients are marginal and also for immobile nutrients. Also, stem girdling or acropetal infection can limit root growth and affect nutrient and water uptake. Plant disease can also infect the vascular system, which can impair nutrient translocation and utilization. Pathogens can also affect membrane permeability or mobilization towards infected sites, which can induce nutrient deficiency or toxicity. *Fusariumoxysporumf. Vasifectum* can increase the concentration of P in leaves, but also decrease the concentration of N, K, Ca and Mg (Huber and Graham, 1999). Since the interaction of nutrients and disease pathogens is complex, I will describe the effect of each nutrient on certain diseases and also the possible mechanism for the tolerance of or resistance to the particular pathogen.

NITROGEN

Nitrogen is the most important nutrient for plant growth and there is an extensive literature about the effect of N on diseases, because its role in disease resistance is quite easily demonstrated (Engelhard, 1989; Marschner, 1995). Despite the fact that N is one of the most important nutrients for plant growth and disease development, there are several reports of the effect of N on disease development that are inconsistent and contradict each other, and the real causes of this inconsistency are poorly understood (Büschbell and Hoffmann, 1992; Marschner, 1995; Hoffland et al., 2000). These differences may be due to the form of N nutrition of the host (Celar, 2003; Harrison and Shew, 2001), the type of pathogen: obligate vs. facultative parasites (Büschbell and Hoffmann, 1992; Marschner, 1995) or the developmental stage of N application (Carballo et al., 1994). Also, there are no systematic and thorough studies about the effect of N supply on disease resistance, on biocontrol agents' activity, and especially on the interaction among nutrient, pathogen, and biocontrol organisms (Tziros et al., 2006). The effect of N is quite variable in the literature. This is due to the different response depending on the type of the pathogen. Regarding the obligate parasites, e.g. *Pucciniagraminis* and *Erysiphegraminis*, when there is high N supply there is an increase in severity of the infection; however, when the disease is caused by facultative parasites, e.g. *Alternaria*, *Fusarium* and *Xanthomonas* spp., high N supply decreases the severity of the infection. However, the situation is more complex for soil borne pathogens as on the root surface there are many more microorganisms than in the bulk soil. Also, there is competition between and repression of different microorganisms, and there are chemical barriers such as high concentration of polyphenols in the rhizodermis and physical barriers such as silicon depositions on the endodermis. The difference between the obligate and facultative parasites is due to the nutritional requirements of the two types of parasites. Obligate parasites require assimilates supplied directly from living cells. In contrast, facultative parasites are semi saprophytes which prefer senescing tissue or which release toxins in order to damage or kill the host plant cells. Therefore, all factors which support the metabolic activities of the host cells and which delay senescence of the host. In the case of obligate fungal parasites the nutritional requirements of the parasites cause changes in the anatomy and physiology of the host plant in response to N. Therefore, the main reason for the increased susceptibility to obligate parasites at high N rates is the various anatomical and biochemical changes together with the increase in the content of the low-molecular-weight organic nitrogen compounds which are used as substrates for parasites. It is believed that plants grown under conditions of low N availability are better defended against pathogens because there is an increase in the synthesis of defense-related compounds (Herms and Mattson, 1992; Hoffland et al., 1999; Wilkens et al., 1996; Hoffl and et al., 2000). However, the response to the N level was different in the facultative parasites, as when the plants were grown under high levels of N they were more resistant to pathogens such as *B. cinerea*. In the case of obligate pathogens such as *Pseudomonas syringae* pv. *tomato*, *Ustilagomaydis* and *Oidiumlycopersicum* increased susceptibility was observed when plants were grown with high N supply (Hoffl and et al., 2000; Kostandi and Soliman, 1991). These reports indicate that disease susceptibility depends on N supply and that the effect of N supply on susceptibility is pathogen-specific. The form of N is also important in plant diseases, and the presence of nitrification inhibitors is important too (Huber and Graham, 1999; Celar, 2003; Harrison and Shew, 2001). At high NO₃ disease is decreased in the case of *Fusariumoxysporum*, *Botrytis cinerea*, *Rhizoctoniasolani* and *Pythium* spp. In contrast, at high NH₄ disease is decreased in the case of *Pyricularia*, *Thielaviopsisbasicola*, *Sclerotiumrolfsii* and *Gibberellazeae*. The form

of N can affect the pH of the soil and also the availability of other nutrients such as Mn. Also, the level of N can affect the phenolics content of plants, which are precursors of lignin. In addition, at high levels of N there is a decrease in Si content, which can affect the disease tolerance. In this case, the subject is quite complex and more research is needed to find a specific mechanism that explains these observations because the interaction between disease and host depends on several factors, including host response, previous crop, N rate, residual N, time of N application, soil microflora, ratio of NH₄ -N to NO₃ -N and disease complex presence.

POTASSIUM

Potassium decreases the susceptibility of host plants up to the optimal level for growth: beyond this point, there is no further increase in resistance which can be achieved by increasing the supply of K and its contents in plants (Huber and Graham, 1999). The high susceptibility of the K-deficient plant to parasitic disease is due to the metabolic functions of K in plant physiology. Under K deficiency synthesis of high molecular- weight compounds (proteins, starch and cellulose) is impaired and there is accumulation of low-molecular-weight organic compounds. Also, K may promote the development of thicker outer walls in epidermal cells, thus preventing disease attack. K can also influence plant metabolism, as K-deficient plants have impaired protein synthesis and accumulate simple N compounds such as amides which are used by invading plant pathogens. Tissue hardening and stomatal opening patterns are closely related to infestation intensity (Marschner, 1995). There were no differences in the crop response in the different sources of K. In addition, the balance between N and K affects disease susceptibility of plants.

PHOSPHORUS

Phosphorus is the second most commonly applied nutrient in most crops and is part of many organic molecules of the cell (deoxyribonucleic acid (DNA), ribonucleic acid (RNA), adenosine triphosphate (ATP) and phospholipids) and is also involved in many metabolic processes in the plant and also in the pathogen. However, its role in resistance is variable and seemingly inconsistent. P has been shown to be most beneficial when it is applied to control seedlings and fungal diseases where vigorous root development permits plants to escape disease (Huber and Graham, 1999). However, in other studies application of P may increase the severity of diseases caused by *Sclerotinia* in many garden plants, *Bremia* in lettuce and flag smut in wheat. Foliar application of P can induce local and systemic protection against powdery mildew in cucumber, roses, wine grapes, mango and nectarines (Reuveni and Reuveni, 1998).

CALCIUM

Calcium is another important nutrient that affects the susceptibility to diseases in two ways. First, Ca is important for the stability and function of plant membranes and when there is Ca deficiency there is membrane leakage of low-molecular weight compounds, e.g. sugars and amino acids, from the cytoplasm to the apoplast, which stimulate the infection by the pathogens (Marschner, 1995). Second, Ca is an important component of the cell wall structure as calcium polygalacturonates are required in the middle lamella for cell wall stability. When Ca concentration drops, there is an increased susceptibility to fungi which preferentially invade the xylem and dissolve the cell walls of the conducting vessels, which leads to wilting symptoms. In addition, plant tissues low in Ca are also much more susceptible than tissues with normal Ca levels to parasitic diseases during storage. Ca treatment of fruits before storage is therefore an effective procedure for preventing losses both from physiological disorders and from fruit

rotting. Adequate soil Ca is needed to protect peanut pods from infections by *Rhizoctonia* and *Pythium* and application of Ca to the soil eliminates the occurrence of the disease. Ca confers resistance against *Pythium*, *Sclerotinia*, *Botrytis* and *Fusarium*. Ca can be mobilized in lesions of alfalfa caused by *Colletotrichum trifolii* and supports the growth of the pathogen by stimulating the macerating action of pectolytic enzyme polygalacturonic acid transeliminase. A putative mechanism by which Ca is believed to provide protection against *Sclerotinia sclerotiorum* is by binding of oxalic acid or by strengthening the cell wall.

OTHER NUTRIENTS

Regarding other nutrients such as sulfur and magnesium, there is not enough information about their role in plant diseases can reduce the severity of potato scab, whereas Mg decreases the Ca content of peanut pods and may predispose them to pod breakdown by *Rhizoctonia* and *Pythium*.

MICRONUTRIENTS

The effect of micronutrients on reducing the severity of diseases can be attributed to the involvement in physiology and Biochemistry of the plant, as many of the essential micronutrients are involved in many processes that can affect the response of plants to pathogens (Marschner, 1995). Micronutrients can also affect disease resistance indirectly, as nutrient-deficient plants not only exhibit an impaired defense response, but often may also become more suitable for feeding as many metabolites such as reducing sugars and amino acids leak outside the plant cell. For example, plants suffering from a Zn deficiency showed increased disease severity after infection by *Oidium* spp. It was also observed that in B-deficient wheat plants, the disease severity was several-fold higher than that in B-sufficient plants, with the fungus spreading more rapidly than in B-sufficient plants. Systemic acquired resistance (SAR) may be involved in the suppression of plant diseases by micronutrients. Reduction in disease severity has been reported in other crops after a single foliar application of H₃BO₃, CuSO₄, MnCl₂ or KMnO₄, which provided systemic protection against powdery mildew in cucumber plants (Reuveni et al., 1997a, b; Reuveni and Reuveni, 1998). The same authors also suggested that application of nutrients such as Mn, Cu and B can exchange and therefore release Ca²⁺ cations from cell walls, which interact with salicylic acid and activate systemic acquired resistance mechanisms. Micronutrients play an important role in plant metabolism by affecting the phenolics and lignin content and also membrane stability (Graham and Webb, 1991). Micronutrients can affect resistance indirectly, as in deficient plants they become more suitable feeding substrate.

MANGANESE

Manganese is probably the most studied micronutrient about its effects on disease and is important in the development of resistance in plants to both root and foliar diseases (Graham and Webb, 1991; Huber and Graham, 1999; Heckman et al., 2003). Mn availability in the soil varies and depends on many and soil biotic factors. Mn is required in much higher concentration by higher plants than by fungi and bacteria and there is opportunity for the pathogen to exploit this difference in requirement (Marschner, 1995). Manganese fertilization can control a number of pathogenic diseases such as powdery mildew, downy mildew, take-all, tansport, and several others (Brennan, 1992; Huber and Graham, 1999; Heckman et al., 2003; Simoglou and Dordas, 2006). Despite the fact that Mn application can affect disease resistance the use of Mn is limited, which is due to the ineffectiveness and poor residual effect of Mn fertilizers on most soils that need Mn supplements, and is because of the complex soil biochemistry of Mn. In most soils that

require addition of Mn such as calcareous soils, 90–95% of added Mn is immobilized within a week. Mn has an important role in lignin biosynthesis, phenol biosynthesis, photosynthesis and several other functions (Marschner, 1995; Graham and Webb, 1991). Mn inhibits the induction of aminopeptidase, an enzyme which supplies essential amino acids for fungal growth and pectin methylesterase, a fungal enzyme that degrades host cell walls. Manganese controls lignin and suberin biosynthesis (Römheld and Marschner, 1991; Vidhyasekaran, 1997) through activation of several enzymes of the shikimic acid and phenylpropanoid pathways (Marschner, 1995). Both lignin and suberin are important biochemical barriers to fungal pathogen invasion (Kolattukudy et al., 1994; Rioux and Biggs, 1994; Hammerschmidt and Nicholson, 2000; Vidhyasekaran, 1997, 2004), since they are phenolic polymers resistant to enzymatic degradation (Agrios, 2005). It has also been shown that Mn soil applications reduce common scab of potato (Keinath and Loria, 1996), *Fusarium* spp. infections in cotton and *Sclerotinia sclerotiorum* (Lib. de Bary) in squash (Graham and Webb, 1991; Agrios, 2005).

ZINC

Zinc was found to have a number of different effects as in some cases it decreased, in others increased, and in others had no effect on plant susceptibility to disease (Graham and Webb, 1991; Grewal et al., 1996). In most cases, the application of Zn reduced disease severity, which could be because of the toxic effect of Zn on the pathogen directly and not through the plant's metabolism (Graham and Webb, 1991). Zinc plays an important role in protein and starch synthesis, and therefore a low zinc concentration induces accumulation of amino acids and reducing sugars in plant tissue (Marschner, 1995; Römheld and Marschner, 1991). As an activator of Cu/Zn-SOD, Zn is involved in membrane protection against oxidative damage through the detoxification of superoxide radicals (Cakmak, 2000). Impairments in membrane structure caused by free radicals lead to increased membrane leakage of low-molecular-weight compounds, the presence of which favors pathogenesis (Graham and Webb, 1991; Marschner, 1995; Mengel and Kirkby, 2001). Application of Zn to the soil reduced infections by *Fusarium graminearum* (Schwabe) and root rot diseases, e.g. caused by *G. graminis* (Sacc.) in wheat (Graham and Webb, 1991; Grewal et al., 1996).

BORON

Boron is the least understood essential micronutrient for plant growth and development, and at the same time B deficiency is the most widespread micronutrient deficiency in the world (Brown et al., 2002; Blevins and Lukaszewski, 1998; Römheld and Marschner, 1991). B has a direct function in cell wall structure and stability and has a beneficial effect on reducing disease severity. In several diseases, however, the function of B in disease resistance or tolerance is the least understood of all the essential micronutrients for plants. The function that B has in reducing disease susceptibility could be because of (1) the function of B in cell wall structure, (2) the function of B in cell membrane permeability, stability or function, or (3) its role in metabolism of phenolics or lignin (Brown et al., 2002; Blevins and Lukaszewski, 1998). Boron promotes stability and rigidity of the cell wall structure and therefore supports the shape and strength of the plant cell (Marschner, 1995; Brown et al., 2002). Furthermore, B is possibly involved in the integrity of the plasma membrane (Marschner, 1995; Brown et al., 2002; Dordas and Brown, 2005). B has been shown to reduce diseases caused by *Plasmodiophora brassicae* (Woron.) in crucifers, *Fusarium solani* (Mart.) (Sacc.) in bean, *Verticillium albo-atrum* (Reinke & Berth) in tomato and cotton, tobacco mosaic virus in bean, tomato yellow leaf curl virus in tomato, G.

graminis(Sacc.) (Graham and Webb, 1991) and *Blumeriagraminis*(D.C.) (Speer) in wheat (Marschner, 1995).

IRON

Iron is one of the most important micronutrients for animals and humans and the interaction between Fe nutrition and human or animal health has been well studied, as it is involved in the induction of anemia. However, the role of Fe in disease resistance is not well studied in plants. Several plant pathogens, e.g. *Fusarium*, have higher requirements for Fe or higher utilization efficiency compared with higher plants. Therefore, Fe differs from the other micronutrients such as Mn, Cu and B, for which microbes have lower requirements. Addition of Cu, Mn and B to deficient soils generally benefits the host, whereas the effect of Fe application is not as straightforward as it can have a positive or negative effect on the host. Fe can control or reduce the disease severity of several diseases such as rust in wheat leaves, smut in wheat and *Colletotrichum musaei* in banana (Graham and Webb, 1991). Foliar application of Fe can increase resistance of apple and pear to *Sphaeropsis malorum* and cabbage to *Olpidium brassicae*. Also, in cabbage the addition of Fe overcame the fungus-induced Fe deficiency in the host but it did not affect the extent of infection (Graham and Webb, 1991; Rohm and Marschner, 1991). In other cases, Fe in nutrient solution did not suppress take-all of wheat and *Colletotrichum* spp. In bean. Application of Fe to disease-suppressive soils increased take-all of barley, and in soils with a high disease score Fe had no effect. Iron can promote antimycosis or interfere with it. Fe does not seem to affect lignin synthesis, even though Fe is a component of peroxidase and stimulates other enzymes involved in the biosynthetic pathway. Fe can activate enzymes that are involved in the infection of the host by the pathogen or the defense, which is why opposite effects were found (Graham and Webb, 1991). Fe can promote synthesis of fungal antibiotics by soil bacteria (Graham and Webb, 1991). Rhizosphere microorganisms can synthesize siderophores which can lower Fe level in the soils. These siderophores can suppress germination of chytrid spores of *Fusarium oxysporum f.sp. cucumerinum* *in vitro*. However, the production of siderophores and the antagonisms for Fe are not only mechanisms to limit the growth of parasitic fungus.

CHLORINE

Chlorine is required in very small amounts for plant growth and Cl deficiency has rarely been reported as a problem in agriculture. However, there are reports showing that Cl application can enhance host plants' resistance to disease in which fairly large amounts of Cl are required, which are much higher than those required to fulfill its role as a micronutrient but far less than those required to induce toxicity (Mann et al., 2004). It has also been suggested that Cl might interact with other nutrients such as Mn. Cl has been shown to control a number of diseases such as stalk rot in corn, stripe rust in wheat, take all in wheat, northern corn leaf blight and downy mildew of millet, and septoria in wheat (Graham and Webb, 1991; Mann et al., 2004). The mechanism of Cl's effect on resistance is not well understood. It appears to be non-toxic *in vitro* and does not stimulate lignin synthesis in wounded wheat leaves. It was suggested that Cl can compete with NO₃ absorption and influences the rhizosphere pH: it can suppress nitrification and increase the availability of Mn. Furthermore, Cl ions can mediate reduction of Mn^{III,IV}oxides and increase Mn for the plant, increasing the tolerance to pathogens.

SILICON

Although Si is the second most abundant element in the earth's soil and is a component of plants it is not considered to be an essential element as defined by Arnon and Stout, except for members of the Equisitaceae family (Marschner, 1995). However, when Si is added to the soil, plants low in soluble Si show an improved growth, higher yield, reduced mineral toxicities and better disease and insect resistance (Graham and Webb, 1991; Alvarez and Datnoff, 2001; Seebold et al., 2000, 2004). Also, in many countries crops such as rice and sugarcane which accumulate high levels of Si in plant tissue are fertilized routinely with calcium silicate slag to produce higher yields and higher disease resistance. Si has been shown to control a number of diseases such as blast (*Magnaporthe grisea*). The mechanism by which Si confers disease suppression is not well understood. It is believed that Si creates a physical barrier which can restrict fungal hyphae penetration, or it may induce accumulation of antifungal compounds such as flavonoid and diterpenoid phytoalexins which can degrade fungal and bacterial cell walls (Alvarez and Datnoff, 2001; Brescht et al., 2004). Except from the essential nutrients for plant growth and development there are a number of other elements that can occur in plant tissue in trace amounts (Li, Na, Be, Al, Ge, F, Br, I, Co, Cr, Cd, Pd and Hg) and have occasionally been linked with host-pathogen relationships: Li and Cd through their marked suppressive effects on powdery mildews are the most noteworthy. Cd was found to inhibit spore germination and development at a concentration of 3 mg kg⁻¹, which is not toxic but elicits a response to infection in the host. Cd and Hg can also promote synthesis of lignin in wheat (Graham and Webb, 1991). The mechanism of Li is not known and it is quite possible that it catalyzes a metabolic pathway which can function as a defense.

EXAMPLES OF DISEASE CONTROL BY NUTRIENTS

There are several examples of disease control through nutrient manipulation which can be achieved by either modifying nutrient availability or modifying nutrient uptake (Huber and Graham, 1999). The most common way to affect the nutrient availability is by using a fertilizer; however, changing the environment through pH modification, tillage, seedbed firmness, moisture control (irrigation or drainage) and specific crop sequences can have a striking effect on nutrient availability. Use of nitrification inhibitors can increase the efficiency and availability of N in high leaching or denitrifying conditions. Addition of microorganisms such as bacteria, fungi which form mycorrhizae and any plant growth-promoting organisms can increase nutrient uptake (P, Zn, Mn) by influencing minor element availability through their oxidation-reduction reactions or siderophore release (Huber and McCay-Buis, 1993). In some cases, the application of fertilizers to the soil is not always effective, such as in the case of Mn, Zn and Fe in high pH soils with high concentrations of free CaCO₃, or where rapid oxidation by microorganisms makes Mn unavailable in the soil. Many times it is recommended to conduct foliar applications which relieve aboveground deficiency symptoms, but Mn is not well translocated in the phloem so that root tissues which are attacked by the pathogens remain Mn-deficient (Huber and McCay-Buis, 1993). Also, addition of nitrification inhibitors with NH₄⁺ fertilizers can suppress Mn oxidation as well as nitrification and increase the availability of Mn, P and Zn for plant uptake. Nutrient uptake can be altered by changing root absorption, translocation and metabolic efficiency, and in some cases it has been shown that wheat seeds with higher Mn content produced plants with less take-all compared with the same cultivars with

a lower Mn concentration in the seed (Huber and McCay-Buis, 1993). Increasing the nutrient content in the grains was actively pursued as a means of improving human nutrition and may concurrently increase plant resistance to a variety of diseases (Graham and Webb, 1991). Some of the most common examples of interaction of nutrients and disease have been the *Streptomyces* scab of potato, *Verticillium* wilt, take-all of wheat, stalk rot of corn, club root of crucifers, fusarium wilt and tissue-macerating disease (Huber and Graham, 1999). *Streptomyces* spp. are strong Mn oxidizers and any cultural technique such as crop rotation, soil amendments with specific crop residues, N fertilizers, soil acidification and irrigation can increase Mn availability and reduce the incidence of the disease. *Verticillium* wilt caused by *Verticillium albo-atrum* and *V. dahliae* is very common and in many cases is one of the most devastating diseases of vegetables, ornamentals, fruits, herbs, field and forage crops. *Verticillium* wilt can be controlled by resistant cultivars, careful crop rotation, sanitation, soil fumigation and nutrient sufficiency, as N, P and K can reduce the disease. Soil fumigation and nitrification inhibitors maintain NH_4^+ in the soil, increase Mn, Cu and Zn and reduce *Verticillium* wilt in tomato. Green manure and flooding the soil to maintain the high moisture content of the soil (known as flood fallowing) can control *Verticillium* wilt in potatoes and tomatoes due to the reduction in inoculum potential and also by increasing the availability of Mn and other nutrients. Take-all is one of the most important diseases of wheat and occurs in many countries of the world. It was found that 12 of the 14 principal nutrients required for plant growth affect take all. Application of N fertilizer and especially NH_4^+ can reduce the losses from take-all: NH_4^+ also increase the availability of Mn, Zn and Fe. Crop rotation can decrease the incidence of the disease. Also, it was found that long-term mono cropping of wheat provides a natural biological control of this disease called take-all decline. Oat can also reduce take-all of wheat. In addition, balanced nutrition, sufficient P and nitrification inhibitors, along with crop rotation, are some of the most effective strategies for reducing take-all in many areas. *Fusarium oxysporum* is an important pathogen which causes vascular wilt in many crops such as vegetable, fruit, fiber and ornamental crops. *Fusarium* wilt is favored by warmer, low-pH soils. In contrast, application of NO_3^- -N fertilizers and application of lime, which reduces the availability of Mn and Fe, increases the pH and results in the reduction of the pathogen.

NUTRIENT MANAGEMENT AND DISEASE CONTROL

Fertilizer application affects the development of plant disease under field conditions directly through the nutritional status of the plant and indirectly by affecting the conditions which can influence the development of the disease such as dense stands, changes in light interception and humidity within the crop stand. It is important to provide a balanced nutrition and at the time when the nutrient can be most effective for disease control and also for higher yield. Not only the application of the fertilizer can affect the disease development, but also anything that affects the soil environment such as pH modification through lime application, tillage, seedbed firmness, moisture control (irrigation or drainage), crop rotation, cover crops, green manures, manures and intercropping.

SYSTEMIC INDUCED RESISTANCE OR SYSTEMIC ACQUIRED RESISTANCE

The induction of resistance reactions of plants against pathogens is a well-known phenomenon in plant pathology. It was first described as a resistance to an attack from a non-virulent pathogen. Thus, it is an enduring, non-specific resistance against pathogens, induced by pathogens that cause a necrotic reaction on the infected leaves, and it is called systemic acquired resistance

(SAR) if the resistance is systemically distributed within the plant. SAR can be induced by a virulent pathogens but also by chemical compounds such as salicylic acid (SA), which is involved in the signal transduction pathway leading to SAR, and also structural analogues of SA can induce SAR. (Wiese et al. 2003) introduced the term chemically-induced resistance (CIR), which is used to describe the systemic resistance after application of synthetic compounds. This resistance is related to the formation of structural barriers such as lignification, induction of pathogenesis related proteins and conditioning of the plants (Graham and Webb, 1991). Systemic induced resistance (SIR) has been found to be induced by foliar sprays of nutrients such as phosphates, K and N. It has been hypothesized that during SIR an immunity signal released or synthesized at the induction site of the inducer leaf is systemically translocated to the challenged leaves, where it activates the mechanisms for defense (Reuveni and Reuveni, 1998). Salicylic acid (SA) has been hypothesized as a possible signal and its exogenous application induces resistance and PR proteins, which typically accompany SIR (Reuveni and Reuveni, 1998). However, SA was found in the phloem sap of non-infected upper leaves when it could not be detected in the phloem sap collected from petioles of the lower leaves infected with *Pseudomonas syringae*. This indicates that SA may not be the primary systemic signal for SIR. A single phosphate foliar application can induce high levels of systemic protection against powdery mildew caused by *Sphaerotheca fuliginea* in cucumbers (Reuveni et al., 1997a, b). A similar response was found in maize, where foliar spray with phosphates induced a systemic protection against common (caused by *Puccinia sorghi*) and northern leaf blight (NLB) (caused by *Exserohilum turcicum*). Trace elements may also play an important role in plants, affecting their susceptibility to fungal or bacterial phytopathogens. Foliar spray with H₃BO₃, CuSO₄, MnCl₂ or KMnO₄ separately induced systemic protection against powdery mildew in cucumber plants. Similar results were found in wheat, where application of B, Mn and Zn separately increased the resistance of plants to tan spot (Simoglou and Dordas, 2006). The mechanism of SIR development is still unknown and it was proposed that the chemicals trigger a release and rapid movement of the “immunity signal” from the infected leaves to the unchallenged ones (Reuveni and Reuveni, 1998). The mechanism might involve an increase in both solute and ionically bound components of peroxidase activity and β -1,3-glucanase in protected leaves above those sprayed with MnCl₂. Mn and Cu might act as cofactors of metallo protein enzymes such as peroxidase, for which Mn ions serve as an inducing agent (Marschner, 1995; Mengel and Kirkby, 2001). Peroxidase and β -1,3-glucanase are involved in the cross-linking of the cell wall components, polymerization of lignin and suberin monomers and subsequent resistance to pathogens. SA is proposed to be a translocatable signal compound in SIR and interacts with intercellular Ca²⁺ in the induction of chitinase in carrot suspension culture. Application of cations such as Mn, Cu and B can increase the Ca²⁺ cations, and interact with SA and activate SIR (Reuveni and Reuveni, 1998). These findings indicate that the mechanism for resistance is present in susceptible plants and it can be induced by simple inorganic chemicals, and that this induced resistance is not pest-specific.

CONCLUSION

In most of the studies reported here the addition of nutrients or application of fertilizers has decreased the incidence of disease in crop plants. This is probably because these nutrients are involved in the tolerance or resistance mechanisms of the host plant. Nutrient application had a much greater effect on reducing disease when the plants were at deficiency levels. Supraoptimal rates of nutrients can also decrease the disease incidence. In cases where the addition of a

nutrient has exacerbated the disease it is possibly because of toxicity rather than deficiency; or in other cases, the addition of a nutrient can aggravate the primary deficiency. Nutrients can reduce disease to an acceptable level, or at least to a level at which further control by other cultural practices or conventional organic biocides are more successful and less expensive.

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