Role of Nutrients in Controlling Plant Diseases in Sustainable Agriculture: A Review

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Abstract In recent years the importance of sustainable agriculture has risen to become one of the most important issues in agriculture. In addition, plant diseases continue to 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 sustainable 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 sustainable 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 Deficiency • Disease resistance • Integrative pest management • Metabolism • Nutrients • Plant physiology • Tolerance • Toxicity

1 Introduction

Sustainability is a term that has been used extensively in recent years in many aspects of our lives, and especially in agriculture because of the effect that certain crop production methods have on the environment (Hanson et al. 2007; Atkinson and McKinlay 1997). Sustainable agriculture is the management and

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utilization of the agricultural ecosystem in a way that maintains its biological diversity, productivity, regeneration capacity, vitality and ability to function, so that it can fulfill – today and in the future – significant ecological, economic and social functions at the local, national and global levels, and that does not harm other ecosystems (Lewandowski et al. 1999).

The sustainability of agriculture has faced some of the most significant challenges in recent years (Hanson et al. 2007; Oborn et al. 2003). Major challenges include: (1) first of all, the rapid growth of the human population and the increased demand for agricultural land and resources, (2) overdependence on fossil energy and the increased monetary and environmental costs of nonrenewable resources, (3) global climate change (Brown 2006; Diamond 2005), and (4) globalization (Hanson et al. 2007). These dominant issues are challenging agriculturists to develop more sustainable management systems like no other time in history. To meet the food and nutritional needs of a growing population, agriculture will need to move beyond the past emphasis on productivity to encompass improved public health, social well-being and a sound environment (Hanson et al. 2007). Also, it is important to find alternative measures to control plant diseases which do not harm the environment and at the same time increase yield and improve product quality (Atkinson and McKinlay 1997; Batish et al. 2007; Camprubí et al. 2007).

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; Huber 1980). 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 sustainable 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). A number of studies showed that it is important with the correct nutrient management to control diseases in order to obtain higher yield (Marschner 1995; Huber and Graham 1999; Graham and Webb 1991 and reference therein). However, there is not enough information regarding the appropriate crop management practices in sustainable agriculture that can reduce yield losses of crop plants due to diseases. There are many factors that can affect the severity of plant disease such as seeding date, crop rotation, mulching and mineral nutrients, organic amendments (manures and green manures), liming for pH adjustment, tillage and seedbed preparation, and irrigation (Huber and Graham 1999). Many of these practices affect the level of nutrients available for the plant and the pathogen, which can affect the disease severity.

It is important to manage nutrient availability through fertilizers or change the soil environment to influence nutrient availability, and in that way to control plant disease in an integrated pest management system (Huber and Graham 1999; Graham and Webb 1991). The use of fertilizers produces a more direct means of using nutrients to reduce the severity of many diseases and together with cultural practices can affect the control of diseases (Marschner 1995; Atkinson and McKinlay 1997; Oborn et al. 2003).

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). Nutrients can affect the growth rate of the host which can enable seedlings to escape/avoid infection when they are at the most susceptible stages. In addition, fertilizers can influence the soil environment and can affect the development of the pathogen. This review aims at summarizing the most recent information regarding the effect of nutrients on disease resistance and tolerance and their use in sustainable agriculture. The main topics will be: (1) nutrition and disease control and role of nutrients in reducing disease severity, (2) nutrient management and disease control, (3) use of cultural methods in improving plant nutrition and disease resistance, and (4) systemic induced resistance or systemic acquired resistance. Also, I will discuss the need for further research on finding how nutrients can affect the mechanisms that are associated with the resistance and tolerance of plants to diseases.

Fig. 1 Powdery mildew (*Erysiphe cichoracearum*) with an extensive growth of white, powdery fungal mycelium on the upper leaf surface of sunflower (*Helianthus annuus*)

2 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 rhizophere, 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 hyperaccumulation 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 (Timonin 1965).

One of the most common symptoms of many soilborne 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. *Fusarium oxysporum f. vasifectum* can increase the concentration of P in leaves, but also decrease the concentration of N, K, Ca and Mg (Huber and Graham 1999).

One of the first observations of the effect of nutrients on disease development was that fertilization reduced disease severity when plants were under deficiency, as fertilization optimized plant growth. When N was applied to cereal crops, take-all (*Gaeumannomyces graminis*) was reduced (Huber and McCay-Buis 1993). Also, P reduced both take-all and pythium root rot infection in cereal crops (Kiraly 1976; Huber 1980). A different trend was observed in the foliar disease of cereal crops, e.g., rust and powder mildew, as increasing N application caused an increase in the incidence of the disease (Figs. 1 and 2). 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.

2.1 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; Huber and Watson 1974; Marschner 1995). Despite

Fig. 2 Damage caused by safflower rust (*Puccinia carthami*)

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 (Huber and Watson 1974; Büschbell and Hoffmann 1992; Marschner 1995; Hoffland et al. 2000). These differences may be due to the form of N nutrition of the host (Huber and Watson 1974; 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., *Puccinia graminis* and *Erysiphe graminis*, 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 (Table 1). However, the situation is more complex for soilborne 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 (Huber 1980). 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 semisaprophytes 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 plant can increase resistance or tolerance to facultative parasites (Agrios 2005; Vidhyasekaran 2004).

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. At high rates there is a higher growth rate during the vegetative stage and the proportion of the young to mature tissue shifts in favor of the young tissues, which are more susceptible. Also, there is a significant increase in amino acid concentration in the apoplast and on the leaf surface, which promotes the germination and growth of conidia (Robinson and Hodges 1981). At high N rates the metabolism of the plant changes: as some key enzymes of phenol metabolism have lower activity, the content of the phenolics decreases and the lignin content may be lower – all these are part of the defense system of plants against infection. In addition, at high N rates Si content decreases (Grosse-Brauckmann 1957; Volk et al. 1958). 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 (Bryant et al. 1983; Herms and Mattson 1992; Hoffland et al. 1999; Wilkens et al. 1996; Hoffland 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*, *Ustilago maydis* and *Oidium lycopersicum* increased susceptibility was observed when plants were grown with high N supply (Hoffland et al. 2000;

Table 1 Effect of N level on disease severity of several diseases

Pathogen or disease		Low N	High N	References
Obligate parasite	*Puccinia graminis*	Decrease	Increase	Howard et al. (1994)
	Erysiphe graminis	Decrease	Increase	Büschbell and Hoffmann (1992)
	Oidium lycopersicum	Decrease	Increase	Hoffland et al. (2000)
	Plasmodiophora brassicae	Decrease	Increase	Kiraly (1976)
	Tobacco mosaic virus	Decrease	Increase	Singh (1970)
	Pseudomonas syringae	Decrease	Increase	Hoffland et al. (2000)
Facultative parasite	*Xanthomonas vesicatoria*	Increase	Decrease	Chase (1989)
	Alternaria solani	Increase	Decrease	Blachinski et al. (1996)
	Fusarium oxysporum	Increase	Decrease	Woltz and Engelhar (1973)

Fig. 3 Tumor-like galls that were formed in corn ears infected by common smut (*Ustilago maydis*)

Kostandi and Soliman 1991) (Fig. 3). 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 NO_3 disease is decreased in the case of *Fusarium oxysporum*, *Botrytis cinerea*, *Rhizoctonia solani* and *Pythium* spp. In contrast, at high NH_4 disease is decreased in the case of Pyricularia, *Thielaviopsis basicola*, *Sclerotium rolfsii* and *Gibberella zeae*. 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 NH_4^+-N to NO_3^--N and disease complex presence.

2.2 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.

Application of K can decrease helminthosporium leaf blight severity and increase grain yields in wheat (Sharma and Duveiller 2004; Sharma et al. 2005). It has been shown that K fertilization can reduce the intensity of several infectious diseases of obligate and facultative parasites (Table 2). It has been frequently

Table 2 Effect of K level on disease severity of several diseases

Pathogen or disease	Low K	High K	References
Puccinia graminae	Increase	Decrease	Lam and Lewis (1982)
Xanthomonas oryzae	Increase	Decrease	Chase (1989)
Tobacco mosaic virus	Increase	Decrease	Ohashi and Matsuoka (1987)
Alternaria solani	Increase	Decrease	Blachinski et al. (1996)
Fusarium oxysporum	Increase	Decrease	Srihuttanum and Sivasithamparam (1991)
Pyrenophora tritici-repentis	Increase	Decrease	Sharma et al. (2005)
Erysiphe graminis	Increase	Decrease	Menzies et al. (1992)

Fig. 4 Light gray lesions with a dark border in sugar beet (*Beta vulgaris*) leaves caused by *Cercospora beticola*

Fig. 5 Lesions caused by bacterial blight (*Xanthomonas campestris* pv *malvacearum*) in cotton (*Gossypium hirsutum*)

observed that K reduces the incidence of various diseases such as bacterial leaf blight, sheath blight, stem rot, sesamum leaf spot in rice, black rust in wheat, sugary disease in sorghum, bacterial leaf blight in cotton, cercospora leaf spot in cassava, tikka leaf spot in peanut, red rust in tea, cercospora leaf spot in mungbean and seedling rot caused by *Rhizoctonia solani* (Figs. 4 and 5) (Table 2) (Huber and Graham 1999; Sharma and Duveiller 2004; Sharma et al. 2005).

2.3 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 (Kiraly 1976). 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). Phosphate fertilization of wheat can have a significant effect and almost eliminate economic losses from pythium root rot (Huber 1980). Similarly, in corn P application can reduce root rot, especially when it is grown on soils deficient in P, and in other studies it can reduce the incidence of soil smut in corn (Huber and Graham 1999; Potash and Phosphate Institute 1988). A number of other studies have shown that P application can reduce bacterial leaf blight in rice, downy mildew, blue mold, leaf curl virus disease in tobacco, pod and stem blight in soybean, yellow dwarf virus disease in barley, brown stripe disease in sugarcane and blast disease in rice (Huber and Graham 1999; Kirkegaard et al. 1999; Reuveni et al. 1998, 2000; Potash and Phosphate Institute 1988). 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

(Huber 1980). 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).

2.4 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 (Huber 1980). Ca confers resistance against *Pythium*, *Sclerotinia*, *Botrytis* and *Fusarium* (Graham 1983). Ca can be mobilized in lesions of alfalfa caused by *Colletotrichum trifolli* and supports the growth of the pathogen by stimulating the macerating action of pectolytic enzyme polygalacturonic acid transeliminase (Kiraly 1976). 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.

2.5 Other Nutrients

Regarding other nutrients such as sulfur and magnesium, there is not enough information about their role in plant diseases. S 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* (Huber 1980).

2.6 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. (Bolle-Jones and Hilton 1956). 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 (Schutte 1967).

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 H_3BO_3, $CuSO_4$, $MnCl_2$ or $KMnO_4$, 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 Ca^{2+} 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.

2.6.1 Manganese

Manganese is probable 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 environmental 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, tan spot, 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). Lignin and suberin are believed to contribute to wheat resistance against powdery mildew and to all diseases caused by *Gaeumanomyces graminis* (Sacc.) (Rovira et al. 1983; Graham and Webb 1991; Huber 1996b; Krauss 1999). 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).

2.6.2 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).

2.6.3 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; Röhmeld 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 *Blumeria graminis* (D.C.) (Speer) in wheat (Marschner 1995).

2.6.4 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 musae* in banana (Graham and Webb 1991; Graham 1983). Foliar application of Fe can increase resistance of apple and pear to *Sphaeropsis malorum* and cabbage to *Olpidium brassicae* (Graham 1983). 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; Röhmeld 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 clamydospores 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.

2.6.5 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 nontoxic *in vitro* and does not stimulate lignin synthesis in wounded wheat leaves. It was suggested that Cl can compete with NO_3^- 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.

2.6.6 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*) in St. Augustinegrass, brown spot (*Cochliobolus miyabeanus* (Ito and Kuribayashi in Ito Drechs ex Dastur) in rice and sheath blight (*Thanatephorus cucumeris* (A.B. Frank) Donk.) in rice, and increase the tolerance of various turfgrasses to *Rhizoctonia solani*, *Pythium* spp., *Pyricularia grisea* (Cooke sacc) and *Blumeria graminis* (DC) (Carver et al. 1998; Savant et al. 1997; Alvarez and Datnoff 2001; Seebold et al. 2000, 2004; Zhang et al. 2006)

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 $3\,\mathrm{mg\,kg^{-1}}$, 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 in defense.

3 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.

3.1 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 $CaCO_3$, 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 NH_4^+ 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 1983; 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, clubroot 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 increases the availability of Mn, Zn and Fe. Crop rotation can decrease the incidence of the disease. Also, it was found that long-term monocropping 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.

4 Use of cultural methods in improving plant nutrition and disease resistance

Not only the application of nutrients as fertilizers can increase the tolerance to the disease, but any measure that can increase the availability and limit the imbalance of certain elements can affect growth and the tolerance of diseases. Most of the approaches that are used in sustainable agriculture have been found to provide a balanced plant nutrition, and at the same time to increase the availability of certain elements and improve the tolerance of plants to disease (Oborn et al. 2003). Approaches such as crop rotation, green manure, application of manures, intercropping and tillage can affect disease resistance and also plant growth. Most of these approaches can significantly increase soil organic matter, which is very important in sustainable agriculture.

4.1 Soil Organic Matter

Soil organic matter (SOM) content and quality affects many soil functions which are related to soil health such as moisture retention, infiltration, release, and also plant health. Field-applied organic residues (crop residues, cover crops and organic wastes) can affect soilborne pathogens and diseases and it is a cultural practice that can affect the availability of nutrients (Stone et al. 2004). Practices such as addition of sphagnum peat, green manures and animal manures have been shown to produce suppressive soils on which pathogens do not establish or persist and do not affect the crop plants. Addition of sphagnum peat to soil has been shown to suppress disease caused by *Pythium* spp. (Hu et al. 1997). Also, addition of different organic amendments has been shown to reduce Phytophthora root rot in a number of species (Hoitink et al. 1977; Spencer and Benson 1982; Szczech et al. 1993; Dixon et al. 1990; Hu et al. 1997). Dairy manure can suppress a number of pathogens in sweet corn (causal agents *Drechslera* spp., *Phoma* spp. and *Pythium arrhenomanes*) and snap bean (causal agents *Fusarium solani* and *Pythium* spp.). There are several mechanisms that are proposed to be involved in biologically and organic material-mediated disease suppression such as microbiostasis, microbial colonization of pathogen propagules, destruction of pathogen propagules, antibiosis, competition for substrate colonization, competition for root infection sites and induced system resistance (or systemic acquired resistance SAR). Soil organic matter (SOM) quantity and quality can affect the plant nutrient status. SOM can impact not only on the total soil nutrient content but also on nutrient availability through the activity of soil microorganisms. Therefore, nutrients can affect disease incidence by increasing plant resistance, improving plant growth (allowing the plant to escape the disease), and influencing the pathogen's environment. Although quantity and quality can have dramatic impacts on soil and plant nutrient content there are only a few studies which focus on soil properties and disease incidence which investigate the contribution of soil or tissue nutrient contents to disease-suppressive effects. Fields with a history of annual organic amendments had higher microbial activity and K contents. Lower NO_3 content and corky root incidence was positively correlated with soil NO_3 and plant tissue N and negatively correlated with soil N mineralization potential, microbial activity, total soil N and soil pH. In another study composed biosolids improved ryegrass establishment, growth and tolerance to leaf rust (caused by *Puccinia* spp.) by improving N nutrition in the amended soil (Loschinkohl and Boehm 2001).

4.2 Crop Rotation and Cover Crops

Crop rotation is the practice of growing a sequence of different crops on the same field. Long-term experiments (more than 100 years) showed that crop rotation together with other fertility management practices are fundamental to long-term agricultural productivity and sustainability (Reid et al. 2001; Stone et al. 2004). The most straightforward principle underlying rotation as a disease control strategy is that plant pathogen propagules have a lifetime in soils and rotation with nonhost crops starves them out (Reid et al. 2001). In bean crops rotation is the most powerful and effective practice to control bean diseases. Crop rotation can increase N levels and can also affect the availability of other nutrients which can affect the disease severity (Reid et al. 2001; Huber and Graham 1999). Also, crop rotation affects the survival of pathogens and it has been used extensively to reduce the severity of many diseases. A nutrient that is affected by crop rotation is Mn: it was found that crop rotation with lupins increases the availability of Mn (Graham and Webb 1991).

Not only crop rotation but also cover crops can change soil chemical, physical and biological properties, including the composition of the soil microbial community, and can therefore reduce or increase the severity of plant diseases. The effect depends on the plant species used and cultivars. Cover crops can increase the content of active OM in the soil, microbial biomass and microbial activity, and contribute to suppression. Cover crops affect the rhizosphere and also the soil microbial community composition and in that indirect way can affect plant health. Crop rotation can influence the severity of soilborne diseases by increasing the buffering capacity of the soil, denying the pathogen a host during the interim of unsuitable species and affecting nitrification, which influences the form of N predominant in the soil (Huber and Graham 1999; Graham and Webb 1991).

Green manure can affect the availability of N and also other nutrients such as P and K. Most of the green manure species that are used can fix N with N-fixing bacteria and can increase soil N levels by $459\,kg\,N\,ha^{-1}$ (Cherr et al. 2006). This can have a significant effect on disease development. Also, green manures can affect the availability of other nutrients such as P, Mn and Zn, which can affect the tolerance of disease (Huber and Graham 1999; Graham and Webb 1991).

4.3 Intercropping

Intercropping systems have the potential to reduce the incidence of diseases (Anil et al. 1998). However, different responses to disease severity with different systems of intercropping have been observed. There are four mechanisms involved in an intercropping system that can reduce disease incidence, all of which involve lowering the population growth rate of the attacking organism:

1. the associate crop causes plants of the attacked component to be poorer hosts.
2. the associate crop interferes directly with the attacking organism.
3. the associate crop changes the environment of the host such that natural enemies of the attacking organism are favored.
4. the presence of nonhost or resistant plants growing in-between susceptible plants can physically block inoculum from reaching the susceptible hosts (i.e., the nonhost serves as a physical barrier to the pathogen inoculum).

Francis (1989) found that intercropping reduced pests and diseases in 53% of experiments and increased them in 18%. The reasons for this increase in pests include reduced cultivation and increased shading, favoring some pests and pathogens; associate species serving as alternative hosts; and crop residues serving as a source of pathogen inoculums. In addition, intercropping was found to improve nutrients by increasing N from legumes, or increasing the uptake of phosphorus and potassium (Anil et al. 1998, reference therein).

4.4 Soil Tillage

Reduced tillage systems or zero tillage can increase SOM content in many agricultural systems. Reduced tillage has the advantage that it conserves SOM, reduces erosion, and reduces energy consumption and production costs (Carter 1994; Fernandez et al. 1999). However, reduced tillage can alter the soil environment and these changes can result in an increase, decrease or no change in disease incidence or severity, depending on the cropping system and disease. Minimum tillage concentrates residues on the soil surface and therefore concentrates the pathogen propagule number on the soil surface: this might or might not impact on disease incidence. Minimum and zero tillage do not disrupt the plant residues in the soil as much as conventional tillage (i.e., since they tend not to bury them), thereby leaving more stubble on the soil surface. The adoption of conservation tillage by farmers has led to an increase in the incidence and severity of many stubble-borne diseases. Standing residues or residues lying on the soil surface are colonized by soil organisms much more slowly and pathogen survival and growth in the undisturbed residues are favored in these systems. Residue-colonizing pathogens are therefore favored over the reduced tillage system and can generate significant yield reduction (Bockus and Schroyer 1998). Conservation-tillage systems concentrate plant residues in the surface soil layer, and microbial biomass and activity are higher in that layer (Dick 1984).

5 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 nonvirulent pathogen. Thus, it is an enduring, nonspecific 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 avirulent 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 noninfected 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 sorgi*) 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 (Graham 1983). Foliar spray with H_3BO_3, $CuSO_4$, $MnCl_2$ or $KMnO_4$ 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 $MnCl_2$. Mn and Cu might act as cofactors of metalloprotein 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 Ca^{2+} in the induction of chitinase in carrot suspension culture. Application of cations such as Mn, Cu and B can increase the Ca^{2+} 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.

6 Future Perspectives

More research is needed in order to find the nutrients or nutrient combinations which can help to reduce disease severity. It is also necessary to find the best integrated pest management approaches with disease-resistant varieties which can be combined with specific cultural management techniques and can efficiently control plant disease. In addition, more research is required to find how the nutrients increase or decrease disease tolerance or resistance, what the changes are in plant metabolism and how this can be used to control plant disease.

It is also important to understand the biochemical pathways by which the nutrients can affect disease. Despite the fact that each nutrient has several functions, mild deficiency can usually be linked to one or more processes that are most sensitive and these processes are linked to the secondary metabolism, which is not immediately necessary for the survival of the organism. The secondary metabolism is involved in the defense against pathogens and some of the roles are well understood and others remain to be elucidated. Also, the evidence that an element has a role in the defense mechanisms not yet regarded as essential in higher plants could lead to recognition of their essentiality. This may require a slight modification of the criteria of essentiality to cover the situation in which yield increases, and indeed survival, are due to the element in question which is manifested only in the presence of a pathogen. This means that such essential elements would not be recognized in disease-free laboratory conditions. The requirement for a key biochemical role would remain.

Systemic induced resistance (SIR) (caused by application of nutrients) could be an alternative strategy to reduce disease severity. In addition, there is a commercially available product containing acibensolar-*S*-methyl (with the commercial name Actigard) that activates the same defense response of SAR. The best SIR will be a chemical which can minimize adverse effects on the host and has high levels of efficacy. NPK fertilizers together with disease-resistant cultivars can be used in this way; however, other nutrients can be used together with NPK in order to reduce disease. In addition, any measure such as crop rotation, application of manures, green manures and cover crops can be used to increase nutrient availability and reduce disease incidence and can be used in the IPM system in sustainable agriculture. Also, the reduction in the crop production cost, the conservation of beneficial biological enemies of pests, preservation of environmental quality and slowing the rate of development of pesticide-resistant strains are some of the benefits that the use of fertilizer can have on IPM and on sustainable agriculture.

7 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. Also, in sustainable agriculture balanced nutrition is an essential component of any integrative crop protection program 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.

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