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Technical Note

The Role of Micronutrients in Controlling Plant Diseases - Knowledge gaps and future research for tree species in particular

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Summary: Mineral nutrients are not only essential for plant growth and development, but also important for plant-disease interactions. In general, plants with optimal nutrition resist or tolerate diseases better than weak, malnourished plants. However, interactions between plants, nutrients, and disease pathogens are very complex and not completely understood. Plant nutrition, although frequently unrecognized, has always been a primary component of disease control. Most soils and environments where plants are cultivated contain an abundance of disease pathogens. On the most basic level, plants suffering a nutrient stress will be less vigorous and more susceptible to a variety of diseases. In this respect, all nutrients affect plant disease. However, some nutrients, especially micronutrients, have a direct and greater impact on plant diseases than others. Due to the very limited research information from tree species, this technote summarizes micronutrients and their interactions with diseases based on agricultural crops. In conclusion, a balance between macronutrients and micronutrients is needed to optimize plant nutrition and maintain plants healthy and tolerant to pests, diseases and other stresses.

Introduction

Mineral nutrients are not only essential for plant growth and development, but also important for plant-disease interactions. In general, plants with optimal nutrition resist or tolerate diseases better than weak, malnourished plants. There are at least 13 mineral nutrients that are essential for normal plant growth and development. These nutrients and their general relative abundance in plants are illustrated in Fig 1. Mineral nutrients are often viewed simply as plant food necessary for better plant growth and yield. Although disease resistance is also controlled by genetics, mineral nutrition can have an influence on plant resistance or susceptibility to pathogens and pests (Rouhana, 2009). In addition, some disease-resistant genes in plants will only activate via specific environmental stimuli (Spann and Schumann, 2013).

Mineral nutrition of plants can be more easily controlled through improved crop management and a better understanding of nutrient supply and demand in agricultural and forestry systems through fertiliser applications. However, how each nutrient affects a

plant's response to disease is unique to each plant-disease complex (Spann and Schumann, 2013).

Although nutrient-pathogen interactions are not well understood, plant nutrients may affect disease susceptibility by changing metabolic pathways that create a more favourable environment for disease. Pathogen infection disrupts and typically alters target or key parts of the plant's physiology, particularly the uptake, transport and use of mineral nutrients. Pathogens may immobilise nutrients in the soil or in infected tissues. Balanced tree nutrition is needed to optimise the growth of high quality and productive forests and maintain healthy trees, tolerant to pests, diseases and other stressors. When certain nutrient elements become deficient or excessive, the balance may tip in favour of certain pathogens or other agents (Fig.1). The mechanisms for this can be: (1) diminished capacity of the tree to provide active or passive defence; (2) increased capacity of the

pathogen to infect and cause disease (Datnoff et al., 2007).

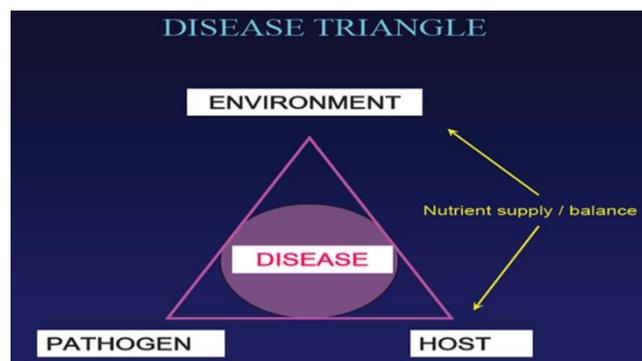


Fig 1. The disease triangle, a framework of the interaction between tree health and influencing mechanisms – nutrient supply.

Plants with optimal nutritional status have the highest resistance (tolerance) to pests and diseases. Susceptibility increases as nutrient concentrations deviate from this optimum. Since the roles of mineral nutrients are well established in host-disease interaction of many crops, tree growers may also better utilise the opportunity of such interactions for improved disease and pest control by mineral nutrition and fertiliser applications. Due to the very limited data from tree species, this technote focuses micronutrients and their interactions with diseases mainly in agricultural crops.

Resistance mechanisms

Understanding how mineral nutrients affect disease resistance in plants is very important for us to complement disease and pest control methods. Altering how plants respond to attacks by pests or diseases can increase resistance. There are three primary resistance mechanisms that mineral nutrition can affect:

1. Formation of mechanical barriers to resist attack primarily through the development of bark, waxy cuticle and thicker cell walls.
2. Synthesis of natural defence compounds such as phytoalexins, antioxidants and flavonoids that provide protection against pathogens.
3. Activation of induced-resistance systems in plants. Systemic acquired resistance and induced systemic resistance are two forms of induced resistance wherein plant defences are preconditioned by prior infection or treatment.

Mineral nutrition affects all three defence systems. A sufficient supply of all nutrients is critical to nutrient management for plant health, performance and sustainability. Similar principles govern the effect of both micronutrients and macronutrients on disease resistance: Any nutritional deficiency hinders plant

metabolism and results in a weakened plant, which lowers disease resistance.

Fungal diseases

Fungal infection occurs as spores germinate on plant surfaces. As germination proceeds, the fungus must penetrate the surface (epidermal) cells, either by passing between the cells or through them. The physical resistance presented by the strength and integrity of the cell walls and intercellular spaces is the plants first line of defence. Nutrients play a major role in the plants ability to develop strong cell walls and other tissue. The germination of spores is stimulated by compounds exuded by the plants. The amount and composition of these exudates is affected by the nutrition of the plant. When plants have low levels of certain nutrients, these exudates will contain higher amounts of compounds such as sugars and amino acids that promote the establishment of the fungus. As a plant becomes infected by a fungus, its natural defences are triggered. The infection causes increased production of fungus inhibiting phenolic compounds and flavonoids, both at the site of infection and in other parts of the plant. The production and transport of these compounds is controlled in large part by the nutrition of the plant. Therefore, shortages of key nutrients reduce the amount of the plants natural antifungal compounds at the site of infection.

Bacterial diseases

Bacterial diseases can be divided into three primary types. Leaf spot diseases, soft rots, and vascular diseases. Leaf spot pathogens typically enter the leaf through the stoma and spread within the intercellular spaces. Since the bacteria do not penetrate the surface of the leaves, the epidermal cell structure or strength is not much of a factor. Plant resistance to bacterial spread within the leaf is closely related to the structure and strength of internal cells and intercellular space, as well as the plants ability to produce and transport antibacterial compounds. These disease-fighting mechanisms are closely related to certain nutrients. Bacterial spread within the host plant is accomplished by the bacteria's production of enzymes that cause the decomposition of pectin (a primary structural component of plant cells). The production and activity of these pectolytic enzymes is inhibited by some nutrients. Additionally, plants suffering from low quantities of those nutrients needed to build proper cell walls and other structural tissue will be subject to greater damage from these pathogens. Bacterial vascular diseases spread by way of the xylem (the vessels that transport water and nutrients from the roots to the leaves). Their presence leads to the formation of "slime" within the vessels, eventually blocking them and leading to wilting and the death of leaves and stems. Certain plant nutrients play a role in blocking or reducing the bacteria's ability to form this slime.

Viral diseases

There is little data on the effects of mineral nutrition on viral diseases. Viruses live and multiply within

plant cells and their nutrition is limited to amino acids and nucleotides found within the cells. Generally, nutrient conditions favourable for good plant growth are favourable for virus multiplication. In some situations, symptoms of viral diseases can be made to lessen or disappear with improved nutrition. However, this appearance does not mean that the virus is not present. For example, sugar beets with beet mild yellowing virus (BMV) exhibit symptoms similar to Mn deficiency. When beets with both Mn deficiency and BMV infection are foliar fertilized with Mn, the visual symptoms of both problems will lessen or even disappear completely. However, work with this combined problem found that the percent of infected plants decreased from 75% in the Mn deficient plants to 40% infection after the Mn deficiency was corrected. While this is a large decrease, there remained a significant infection in the field. The primary vectors carrying virus to a crop are sucking insects, such as aphids, and fungi. Plant nutrition can affect both fungi and some insects, thus affecting the viruses that they may carry. It has been found that the nutrient status of a plant can affect the aphid population on plants. For example, it was found in 1965 that certain aphids tend to settle on yellow reflecting surfaces, such as chlorotic leaves caused by nutrient deficiency. Feeding intensity and reproduction by sucking insects tend to be higher on plants with higher amino acid content. This condition is typical of plants suffering certain nutrient stresses. As you will read in the section on silicon, application of this non-nutrient element has been shown to physically inhibit the feeding ability of some sucking insects like aphids. In studies with watercress, it was reported that high levels of Zn fertilization improved control of the "crook rot" fungus which is also a vector for the chlorotic leaf spot virus. Therefore, the high Zn fertilization controlled both a fungus and a virus.

Effect of micronutrients on plant diseases

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 defence 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+} 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 contents of phenolics and lignin, and membrane stability as well (Graham and Webb 1991). Micronutrients can affect resistance indirectly, as in deficient plants they become more suitable feeding substrate.

Boron (B)

B deficiency is the most widespread micronutrient deficiency in the world. But B is the least understood essential micronutrient for plant growth and development, and disease resistance or tolerance. B has a direct function in cell wall structure and stability and has a beneficial effect on reducing disease severity. The function that B has in reducing disease susceptibility could be due to its (1) role in the formation of carbohydrate-borate complexes, which control carbohydrate transport and cell wall structure, (2) function in cell membrane permeability or stability, and (3) role in the metabolism of plant defence compounds such as phenolics and lignin.

When a plant becomes infected by a fungus, its natural defences are triggered. The infection causes increased production of fungus inhibiting phenolic compounds and flavonoids, both at the site of infection and in other parts of the plant. The production and transport of these compounds is controlled in large part by the nutrition of the plant. Therefore, shortages of key nutrients such as K, Mn, Cu, Zn, and B reduce the amount of the plants natural antifungal compounds at the site of infection. It has been demonstrated that when B is deficient, plant cell walls tend to swell and split, and to result in weakened intercellular space. This results in a weakened physical barrier to initial infection and expansion of the infection. With a shortage B, the plant exudates contain higher amounts of compounds such as sugars and amino acids that promote the establishment of most fungal infections.

Boron has been beneficial in the control of the diseases by *Plasmiodiophora brassicae* (Woron.) in crucifers, *Fusarium solani* (Mart.) Sacc. in bean, *Verticillium albo-atrum* Reinke and Berth in tomato and cotton, tobacco mosaic virus in bean, tomato yellow leaf curl virus in tomato, *Gaeumannomyces graminis* (Sacc.) and *Blumeria graminis* (D.C.) (Speer) in wheat.

Manganese (Mn)

Mn is probably the most studied micronutrient about its effects on plant disease and has long been known to contribute to the suppression of fungus and bacterial diseases. Mn plays a key role in the production of phenolic compounds and lignin and suberin formation through activation of several enzymes of the shikimic acid and phenylpropanoid pathways. Phenolic compounds are toxic to many

disease pathogens. Both lignin and suberin are important biochemical barriers to fungal pathogen invasion. When a plant becomes infected by a fungus, its natural defences are triggered. The infection causes increased production of fungus inhibiting phenolic compounds and flavonoids, both at the site of infection and in other parts of the plant. 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.

Plants also respond to fungal infection by forming oxygen radicals and hydrogen peroxide, both of which help to fight infections. Mn plays a role their formation and later detoxification. It is commonly found that diseased plants have much lower Mn content than healthy plants. In Norway spruce, the inner bark of roots is less capable of fungistatic activity against the pathogen *Fomes annosus* than is the outer bark. When this disease is established, it leads to heart root disease by affecting this weaker area of the roots. When these trees are supplied with high Mn and low N, the fungistatic capability of the inner bark increases. Mn has been beneficial in the control of the fungal or bacterial diseases in potato, rice wheat, cotton, swede, squash, avocado and Norway spruce.

Copper (Cu)

Using Cu for disease prevention and correction was well known by 1900, about 30 years before it was determined to be an essential nutrient. Like Mn, Cu is an essential nutrient for higher plants as well as fungi and bacteria. Cu is also very toxic to all plant forms when present at high levels. However, higher plant forms such as crops and ornamentals can tolerate much higher Cu levels than lower forms, such as fungi and bacteria. This difference in tolerance enables growers to use Cu as a disease treatment. Cu fertilization has decreased the severity of a wide range of fungal and bacterial diseases. While Cu is known to control diseases when foliar applied, many times foliar diseases were controlled with soil applications of Cu.

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Research into the fungicidal properties of Cu has been conducted using foliar applications that are 10 to 100 times as high as those recommended for foliar

fertilization. However, it has been demonstrated that plants which have low tissue levels of Cu (by nutrient standards) are more susceptible to various diseases. Therefore, the disease suppression capabilities of Cu can be said to occur over a wide range of concentration, and to function both as a direct inhibitor to various diseases as well as enabling plants to better defend themselves from disease. Cu has been beneficial in the control of more than 15 plant diseases, including *Eucalyptus marginata* root rot by *Phytophthora cinnamomic*.

Zinc (Zn)

Early studies indicate that Zn improves a plants ability to defend itself from diseases. Today, information on the specific relationship of Zn to plant pathogens is somewhat mixed. Some sources suggest that there is no clear evidence to explain how Zn suppresses some diseases, while others indicate that Zn is directly toxic to many disease organisms. The fact that Zn is an active ingredient in some fungicides is evidence that it is directly toxic to some pathogens. Evidence also indicates that soils low in soluble Zn are more likely to support higher populations of some diseases causing organisms.

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. As an activator of Cu/Zn-SOD, Zn is involved in membrane protection against oxidative damage through the detoxification of superoxide radicals. Impairments in membrane structure caused by free radicals lead to increased membrane leakage of low-molecular-weight compounds, the presence of which favours pathogenesis.

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. Zn has been beneficial in the control of about 30 plant diseases, including powdery mildew of rubber trees by *Oidium heveae*, crown and root rot of *Eucalyptus* by *Phytophthora cinnamomic*, and wood rot of various trees by *Stereum strigosazonatum*.

Iron (Fe)

Fe 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. However, the role of Fe in disease resistance is not well studied in plants. While there is some evidence that Fe is active against some diseases, it is not considered in the same category as K, Mn, Cu, or Zn. Evidence suggests that plant pathogens generally have a high requirement for Fe. Some work suggests that the competition for Fe between higher plants and pathogens is a factor in the infection of higher plants. It is not clear if plants use the competition for Fe as a defence mechanism against disease.

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. Foliar application of Fe can increase resistance of apple and pear to *Sphaeropsis malorum* and cabbage to *Olpidium brassicae*. In addition, the addition of Fe overcame the fungus-induced Fe deficiency in the host but it did not affect the extent of infection in cabbage. 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. In summary, Fe has been beneficial in the control of some diseases. In most cases, the beneficial effects required foliar Fe applications, some at high concentrations.

Silicon (Si)

Si is the second most abundant element in the earth's soil and is a component of plants, but it is not considered to be an essential element. Si can be beneficial in reducing disease in some plants. 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. 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).

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. Increased Si in plants has been shown to increase the difficulty of sucking insects, like aphids or leaf hoppers. Decreased feeding by these insects could also aid in the prevention of the spread of viral diseases that could be transmitted by the insects.

Molybdenum (Mo)

Little is known about the effects that Mo may have on plant diseases. It has been reported that Mo applied to tomato roots reduced the symptoms of *Verticillium* wilt and that Mo reduced the production of a toxin by *Myrothecium roridum*, a pathogen of muskmelon. A report indicated that Mo "slightly" decreased the reproduction of *Phytophthora cinnamomi* and *Phytophthora dreschleri* diseases of a variety of crops. Another report indicated that soil applications of Mo decreased the populations of the nematode *Rotylenchulus reniformis*, which infects various crops. It is not known whether Mo within a plant plays any role in protection against diseases. It is possible

that any effect of Mo deficiency on plant diseases may be indirect, through its role in N metabolism.

Cobalt (Co)

Co is an essential nutrient in bacteria and animals, but not in plants. Excess Co causes toxicity symptoms in plants, ranging from diffuse leaf chlorosis and necrosis in tomato, to reduced biomass accumulation and nutrient uptake in cauliflower. However, Small amounts of Co have beneficial effects on the growth of leguminous plants, such as *Pisumsativum* and *Lupinus angustifolius*, resulting from enhanced nodule activity. This is because Co is required as a cofactor for the coenzyme cobalamin in *Rhizobium spp.* during nodulation, nitrogen fixation and leghemoglobin synthesis (DalCorso et al., 2014). Soybeans grown without Co are severely retarded in growth and exhibit severe nitrogen deficiency, leading to death in about one of four plants.

Knowledge gaps and future research

For tree species, little research has been done on the role of micronutrients in controlling plant diseases and their interactions with other environmental factors. There are many knowledge gaps on the relationships between tree nutrition and diseases and the underlying mechanisms for the control of micronutrients in tree diseases.

Several studies have shown that mineral nutrition (either micronutrients or macronutrients) can have dramatic effects on pathogen caused losses on the field. However, the underlying mechanisms are poorly understood. Owing to the high throughput genotyping and phenotyping techniques, the exploration of natural diversity in terms of mineral profiles (ionomic profiles) and tolerance to pathogens could provide valuable data on the possible correlations between mineral uptake capacities of a genotype and its tolerance to a biotic stress. To cope with mineral needs and protect themselves against pathogens, plants benefit from microbes that colonize their rhizosphere, phyllosphere as well as from endophytic microbes. Some of these microorganisms enhance both plant nutrition and immunity. The molecular characterization of the underlying cross talk mechanisms between these two processes could be of great value to optimize their use. Invading pathogens use different strategies to obtain minerals from their hosts and can use the host mineral contents as a signal to activate virulence factors making some of the virulence factors potential targets for disease control. Alternatively, they can compete with the beneficial microflora for some minerals. Thus, investigating the mechanisms involving mineral uptake by pathogens can be of great interest to have a comprehensive view of the overall process involving minerals as key players in plant health.

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 genotypes that can be combined

with specific silvicultural 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.

To defend themselves against pathogens, plants accumulate antimicrobial compounds, strengthen their cell walls and activate stress-signalling cascades. It is also important to understand the biochemical pathways by which the nutrients can affect disease. The secondary metabolism is involved in the defence against pathogens and some of the roles are well understood and others remain to be elucidated. Systemic induced resistance (SIR) (caused by application of nutrients) could be an alternative strategy to reduce disease severity.

To develop robust plant disease management through balanced nutrition, some future research are recommended as follows:

- Role of plant genes involved in mineral homeostasis in plant-pathogen interactions including in the regulation of the molecular processes of plant immunity (effector triggered immunity, pattern triggered immunity).
- Mechanisms by which mineral nutrition affects disease susceptibility/resistance.
- Correlations between mineral nutrition capacities and susceptibility/resistance by exploring natural diversity.
- Mechanisms underlying the capacity of a beneficial microbe or microbial community to enhance both tolerance to biotic stresses and mineral nutrition efficiency.

Conclusions

In conclusion, all essential nutrients are critical for the proper metabolic functioning of forest trees. A balance between macronutrients and micronutrients is needed to optimize growth of high quality forests and maintain trees healthy and tolerant to pests, diseases and other stresses.

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