Review

Mineral nutrition in the control of nematodes

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Although plant tolerance and resistance to pathogens are genetically controlled, they are significantly influenced by environmental nutrition factors. Mineral nutrients can increase or decrease resistance or tolerance to pathogens and pests. Plants receiving ample nutrition have higher resistance to diseases and higher tolerance. This is based on the fact that more vigorous plants have greater capacity to offset a loss of photosynthates, for instance, or reduction in root and leaf surface area caused by infection by pathogens or poor nutrition. In this context, plant mineral nutrition can be considered an environmental nutrition factor that can be manipulated relatively easily, and is an important component in disease control, as well as a tool for managing phytonematodes, reported to be causing losses in countless important agricultural crops. Thus, the aim of this review was to discuss the importance of plant mineral nutrition in the control of phytoparasitic nematodes.

Key words: Management, plant nutrition, phytonematodes, resistance.

INTRODUCTION

Plant nutrition is a uniquely important factor in fostering life on earth, which in all its variety is still made up of atoms of chemical elements. The basic reservoirs of these elements are rocks, oceans and the atmosphere. If one of the chemical elements essential to plant life is not available in sufficient quantity or is present in chemical combinations that are difficult to absorb, the deficiency of this element will cause disruptions in plant metabolic processes. The occurrence of these disruptions and identification of nutrient deficiencies and their causes, as well as the toxic effects of excessive concentrations of certain elements, highlights the functional roles of these elements in plant metabolism (Epstein and Bloom, 2004).

Generally, speaking, under field conditions, the application of fertilizers affects the incidence of diseases and pests induced by the plants' nutritional status and indirectly produce dense stands and alterations in the interception of light and moisture within the crop (Agrios, 2005). The numerous effects of plant nutritional status and fertilizer use on diseases and pests are directly relevant to the control of these organisms by chemical means. The application of mineral fertilizer replaces or reduces the need for chemical control in some cases, whereas in others it can increase this need. For instance, chemical control is essential in the presence of high levels of nitrogen (Marschner, 1997).

In general, nutrients can directly or indirectly predispose plants to pathogen attack. They can reduce or increase disease severity, affect the environment to attract or deter pathogens and also induce resistance or

tolerance in the host plant (Zambolim et al., 2001; Agrios, 2005). Applying fertilizer can, partially, offset nematode-induced damage by stimulating plant development (Ferraz et al., 2010). The general rule is that, if a nutrient is essential to a plant species, it should be supplied in balanced proportion to other essential nutrients, since deficiency can aggravate disease, especially in short-cycle crops (Zambolim et al., 2001).

Nematodes are among the pathogens that can be affected by plant nutrition. They are very small, almost transparent organisms that easily escape detection by the farmer. On penetrating the plant and feeding on its tissues, they draw off its nutrients and cause mechanical damage and physiological changes by injecting toxins (Cadet and Spaull, 2005). The symptoms of nematode attack vary according to the species, and mainly take the form of galls produced by *Meloidogyne* spp., cysts caused by *Heterodera* spp. and root lesions caused by the genus *Pratylenchus*. However, other symptoms can be presented, such as very poor root systems, peeling or tearing of the cortex and tuber necrosis (Agrios, 2005; Cadet and Spaull, 2005; Ferraz et al., 2010). These symptoms are often mistaken for abiotic problems or outbreaks of other pathogens (Agrios, 2005). In the aerial part, the main symptoms are a reduction in plant growth due to nutrient deficiency, wilting during the hottest times of day and a fall in crop yield, generally due to root damage that lowers the plant's capacity to absorb water and nutrients (Cadet and Spaull, 2005; Decraemer and Hunt, 2006; Ferraz et al., 2010).

Phytoparasitic nematodes upset the balance of agroecosystems and impose limits on the yields of numerous crops, such as cotton, maize, soybean, sugarcane and vegetables (Bond et al., 2000; Dinardo-Miranda et al., 2000; Barros et al., 2005; Barbosa et al., 2010; Obici et al., 2011; Dias-Arieira et al., 2012a). The nematode control is complex and the best results are obtained by integrated management.

In the soil, nematodes are attracted to their hosts by the concentration gradient formed by root exudates, which provide a recognition signal, but can also repel nematodes. However, it is not clear whether mineral nutrients play an important role in this process. Some studies show that nematodes cause a drop in root system activity and growth (Oteifa and Elgindi, 1976; Merwin and Stiles, 1989). For example, nematodes are cited as the main agents responsible for potassium deficiency in apples (Merwin and Stiles, 1989). In cotton, attack by *Rotylenchulus reniformis* Linford and Oliveira can cause significant losses, but does not affect cotton plant aerial part growth in the presence of high levels of available potassium (Oteifa and Elgindi, 1976). Similar responses have also been observed for micronutrients (Huber and Wilhelm, 1988).

Greenhouse studies have shown that applying macronutrients to sugarcane reduces the severity of the disease caused by *Meloidogyne* spp., allowing the plant to develop normally (Asano and Moura, 1995). In contrast, the same study showed that there was no observed effect for micronutrients on plant development, or on nematode reproduction. Therefore, it is possible that interactions involving *Meloidogyne* spp. and macronutrient deficiencies are responsible for more severe meloidogynosis in sugarcane on the coastal plateaus of northeastern Brazil.

Among plant nutrients, nitrogen is essential for growth and yield. An abundance of nitrogen results in the production of new tissues and saps, and can extend the vegetative state and increase the number of feeding sites in the roots, encouraging nematode attack. On the other hand, a plant that is deficient in nitrogen can become debilitated, suffer slowed growth and become more susceptible (Zambolim et al., 2001; Ferraz et al., 2010). However, the form in which the nutrient is available, whether ammonium (NH_4^+) or nitrate (NO_3^-), has more effect on the severity of the nematode attack than the quantity of nitrogen available (Table 1) (Ferraz et al., 2010).

Nitrogen in ammonium form, present in fertilizers and organic matter, is more prejudicial to nematodes than in nitrate form due to the release of free ammonia (NH_3) into the soil during its decomposition (Rodríguez-Kábana et al., 1981; Rodríguez-Kábana, 1986). The nematicidal property of ammonia is mainly attributable to its plasmolytic effect around the point at which it is applied to the soil (Rodríguez-Kábana, 1986). Nevertheless, other indirect mechanisms, such as an increase in microbiota antagonistic to nematodes, may also have a significant effect. Many fungi in the soil prefer nitrogen in ammonium form (Rodríguez-Kábana et al., 1981), which means that ammonia-producing materials should encourage the proliferation of nematode parasitic fungi. Because of the nematicidal effect of ammonium nitrogen, urea has also been the subject of many studies, since it is rapidly converted into ammonia by the action of urease in the soil (Rodríguez-Kábana, 1986). Urea is a good nematicide when applied in at doses higher than 300 kg N ha^{-1}. However, doses at this level can be phytotoxic due to the low C : N ratio. Therefore, applying urea in conjunction with a supplementary source of carbon is a viable method of controlling nematodes as well as reducing the phytotoxic effect of the fertilizer (Huebner et al., 1983).

Working with mixtures of urea and molasses to control *Meloidogyne arenaria* (Neal) Chitwood in soil cropped with *Curcubita pepo* L., Rodríguez-Kábana and King (1980) found that it was possible to reduce the severity of nematode attacks using urea alone. The authors also reported that the results represent a specific case in which the NH_3 supplied prevents the urease in the soil from acting on the urea, resulting in the release of NH_3 and CO_2. Since the action of the urea in the soil is dependent on the urease (Kandeler and Gerber, 1988), any treatment that results in the formation of the enzyme

Table 1. Effect of different nutrients on some species of nematode.

Host	Nematode	NO_3^-	NH_4^+
Soybean	*Heterodera glycines* Ichinohe	Increases severity	Reduces severity
Tobacco	*Globodera* spp.	Increases severity	Reduces severity
Cucumber	*Meloidogyne* spp.	Increases severity	Reduces severity
Common bean	*M. incognita* (Kofoid and White) Chitwood	Increases severity	Reduces severity

Source: Adapted by Zambolim et al. (2001).

can increase the efficacy of chemicals in combating nematodes. Therefore, the addition of a source of carbon (molasses) stimulated the production of urease and improved the efficacy of the urea against *M. arenaria*, possibly by stimulating the activity of biological control agents (Rodríguez-Kábana and King, 1980). The authors also mention the possibility of using nitrification inhibitors to increase the efficacy of treatments, with the aim of reducing the quantity of urea necessary to produce nematicidal activity, significantly cutting treatment costs.

Phosphorus is essential to plant growth and can also influence diseases caused by nematodes (Ferraz et al., 2010). Plants with high levels of phosphorus, release fewer root exudates and are therefore less attractive to nematodes cutting decreasing the incidence of the diseases (Marschner, 1997). Furthermore, plants become more resistant when supplied with sufficient quantities of phosphorus (Zambolim et al., 2005), as a result of increases in protein synthesis, cell activity and production of polyphenols, peroxidase and ammonia (Wang and Bergeson, 1974). The effect of phosphorus in the control of nematodes can vary depending on the source used. Application of phosphorus in the form of triple superphosphate was more effective in controlling *Pratylenchus scribneri* Steiner than single superphosphate when used on soybean, maize and cotton (Collins and Rodríguez-Kábana, 1971).

Phosphite has been widely used in agriculture for the countless advantages that it has, mainly in increasing the absorption of phosphorus by the plant compared to phosphate-based products. Furthermore, it has other interesting features, such as boosting microbial activity (Cohen and Coffey, 1986) and activating plant defense mechanisms (Jackson, 2000).

In a study conducted by Dias-Arieira et al. (2012b), potassium phosphite was effective in cutting the population of *Pratylenchus brachyurus* and Filipjev and Schuurmans Steckhoven in maize. Similar results have been reported for other nematode species (Oka et al., 2007). The efficacy of phosphite in the control of microorganisms is attributed to 2 factors. The first is direct microbial activity against phytopathogens (Guest and Grant, 1991). However, in the study conducted by Dias-Arieira et al. (2012b), the phosphite was applied to the aerial part of the plant, that is, spatially separated from the nematode, and in this case its efficacy was related to a second factor, its capability of stimulating plant defense mechanisms, such as the production of phytoalexins (Derks and Creasy, 1989). This hypothesis finds further support in the study conducted by Salgado et al. (2007) in which potassium phosphite boosted the hatching of *Meloidogyne exigua* Goeldi, but did not kill off juveniles, that is, it had no direct action on the parasite. In addition, Oka et al. (2007) reported that potassium phosphite applied to the aerial part was effective in controlling *Heterodera avenae* Wollenweber and *Meloidogyne marylandi* Jepson and Golden in wheat and oats. This result is attributable to phosphite's ability to translocate along the plant's xylem and phloem (Quimette and Coffey, 1990).

Although, potassium (K) is the most abundant cationic mineral in plants, it is not an integral part of any metabolite that can be isolated in vegetal matter. However, it is present in high concentrations in the cytosol and vacuole as a free ion (K^+). In addition to playing an important role in enzymatic activation (over 60 enzymes), potassium also participates in membrane crossover, neutralization of anions and maintaining membrane potential (Epstein and Bloom, 2004).

It is thought that adequate plant nutrition with potassium helps reduce the incidence of disease due to increased resistance to the penetration and development of pathogens (Huber and Arny, 1985; Perrenoud, 1990), and is considered the nutrient that has the greatest influence on diseases (Perrenoud, 1990). The increase in plant resistance in the presence of plentiful supplies of potassium is mainly due to the increased thickness of the epidermal cell wall, boosting the structural rigidity of tissues and playing a fundamental role in many metabolic reactions in plants, regulating stomata functioning and promoting rapid recovery of injured tissue, due to the accumulation of phytoalexins and phenols around the infection site (Huber and Arny, 1985).

Barbosa et al. (2010) evaluated the use of potassium fertilizer (single and multiple doses) on populations of *H. glycines* in resistant and susceptible soybean cultivars and observed that increasing doses of potassium reduced the number of females in the root system and the nematode reproduction factor in the susceptible cultivar. Similarly, in an experiment developed by Pinheiro et al. (2009), doses of potassium significantly influenced the number of cysts pot[-1], eggs cyst[-1], females

and cyst per root system and the reproduction factor of *H. glycines* in soybean. This reduction is thought to be due to the interference of the potassium in the reception of the signal by the cell membrane, reducing the number of syncytia (Barbosa et al., 2010). Potassium fertilizer also reduced nematode multiplication in the pathosystems of *M. exigua-Coffea arabica* L. (Santos, 1978). On the other hand, this kind of fertilizer boosted increased populations of *Tylenchulus semipenetrans* Cobb in *Citrus aurantium* L., *R. reniformis* in *Vigna sinensis* Endl. (Badra and Yousif, 1979), and *R. reniformis* in cotton (Pettigrew et al., 2005), a fact result that has been attributed to the stronger growth of the plant's root system.

Calcium (Ca) performs a number of functions in plants. In quantitative terms, it is the predominant nutrient in the apoplast, where it has at least 2 separate functions: a) interlinking pectin chains and therefore contributing to their stability, and b) affecting the mechanical properties (rheology) of the pectin gel. It is an essential element for the integrity of the plant cell's plasmatic membrane, and more specifically ion-transport selectivity (Epstein and Bloom, 2004). Like other nutrients, calcium must be present in sufficient quantity in the soil, since calcium-deficient plants are more susceptible to nematode attack (Hurchanik et al., 2003).

The calcium content of plant tissues can affect the incidence of diseases in two ways: a) when calcium levels are low, there is an increase in the efflux of compounds of low molecular weight (sugars) from the cytoplast to the apoplast, and b) calcium polygalacturonates are required for the middle lamella to stabilize the cell wall. Calcium plays a critical role in cell division and development, in the structure of the cell wall and in the formation of the middle lamella (Huber, 1991). Many phytopathogenic agents reach the plant tissue by producing extracellular pectolytic enzymes, such as galacturonase, that degrade the middle lamella (McGuire and Kelman, 1986), and the enzyme activity is dramatically inhibited by the presence of calcium (Marschner, 1997).

Application of calcium carbide (CaC_2) was effective in reducing the number of galls, egg masses and juveniles of *M. incognita* in zucchini (*Cucurbita pepo* var. Melopepo), regardless of the concentration used, increasing crop yield (Mohamed and Youssef, 2009). However, the form in which calcium is most widely used consists of liming, which is directly link to soil pH. Rocha et al. (2006) evaluated the effect of increasing doses of lime on the population of *H. glycines* in soybean roots and found that the number of females dropped as lime doses were increased, up to 3.039 t ha^{-1}. The authors concluded that increasing the supply of calcium boosted the resistance of the cells, lowering root infection by the nematode. On the other hand, Anand et al. (1995) reported that higher pH values (6.5 and 7.5) resulted in higher populations of *H. glycines* in soil with a pH of 5.5. The authors explain that soils with pH values of 6.5 and

7.5 are more favorable to soybean growth, resulting in stronger increasing root development and consequently better conditions for the development of infection sites.

Soil pH seems to be important for nematode activity, although the probable effects are indirect, due to the alteration of the microbiota in the soil and the availability of micronutrients to plants (Rocha et al., 2006). High pH values and base saturation were favorable to *H. glycines* in soybean crops in the municipalities of Chapadão do Sul and Chapadão do Céu, Brazil, where pH values higher than 6.0 intensified the damage caused by the nematode and immobilized micronutrients in the soil, causing deficiencies in the plants and reducing natural parasitism on eggs and cysts (Silva et al., 1997).

Silicon (Si) is among the most abundant nutrients in the earth's crust, existing in quantities second only to oxygen. The majority of soils are predominantly silicates and aluminosilicates. Plants absorb silicon in variable quantities, and the usual amounts of silicon found in dry plant matter range from around 0.1 to 10.0% (Epstein and Bloom, 2004). Silicon has been researched especially as an inducer of plant resistance to diseases (Rodrigues and Datnoff, 2005). It can induce the plant's defense mechanisms by activating the synthesis of substances such as phenols, lignin, suberin and callose in the cell wall.

The mechanism by which silicon activates resistance has yet to be fully elucidated. The way in which silicon is deposited in the cell wall has given rise to the hypothesis of a possible physical barrier, by the ascending movement of the element from the roots to the leaves, undergoing polymerization in the extracellular spaces in the cell walls and the xylem vessels (Terry and Joyce, 2004). According to Epstein and Bloom (2004), plants absorb silicon, transporting it rapidly to the aerial part and when transpiration takes place, the dissolved silicon becomes supersaturated and can polymerize and form solids, known as opals or opal phytoliths. Incorporation of these phytoliths at the end of the respiratory flow of water in the cell walls makes them rigid. Although the majority of the silicon in plants is polymerized or solidified, the role of this element in resistance to diseases is mainly due to the silicon fraction in solution inside the plant, suggesting that defensive compounds are synthesized in the dicotyledons.

Silva et al. (2010) studied the silicon-mediated biochemical resistance responses of coffee to *M. exigua* and presented evidence indicating that the reproductive capability of the nematode in coffee roots supplied with silicon was adversely affected. The response was associated with the production of lignin and an increase in the activity of peroxidase (POX), polyphenol oxidase (PPO) and phenylalanine amonialiase (PAL), especially in the susceptible cultivar evaluated. According to Guimarães et al. (2008), potassium silicate was effective in inducing sugarcane resistance to *M. incognita*, since it reduced the number of pathogen eggs in the RB867515

and RB92579 varieties. However, it did not affect the aerial part biomass of the RB867515 and RB863129 varieties, nor the population density of *Pratylenchus zeae* Graham in the soil, 100 days after transplanting. Dutra et al. (2004) reported a greatest decrease in the number of galls and eggs of a number of species of *Meloidogyne* in common bean, tomato and coffee treated with calcium silicate.

In contrast to other heavy metal ions such as copper, iron and manganese, zinc (Zn) is a divalent cation (Zn^{2+}) that does not undergo valency exchange and, therefore, has no redox activity (Epstein and Bloom, 2004). Over 80 proteins containing zinc have been reported. Many enzymes require zinc at the active site, as occurs in carbonic anhydrase, superoxide dismutase (together with copper) and alcohol dehydrogenase. In other enzymes, zinc is an integral component of the protein but is not near the active site. Zinc ions regulate the conformation of the protein domain which connects to the DNA. This means that zinc deficiency seriously interferes with growth, which is dependent on protein synthesis, which in turn depends on transcription (Barker and Pilbeam, 2007). These considerations suggest that one of the inhibiting effects of zinc deficiency on growth could be due to inadequate protein synthesis (Epstein and Bloom, 2004).

Plants deficient in zinc contain low levels of superoxide dismutase and therefore high levels of superoxide radicals, promoting membrane lipid peroxidation and a loss of membrane integrity, increasing permeability (Barker and Pilbeam, 2007). Furthermore, the accumulation of free amino acids and amides occurs as a result of protein synthase inhibition due to zinc deficiency, boosting the quantity of these amino acids in root exudates (Cakmak and Marschner, 1988). Since nematodes are attracted by exudates, the higher root exudation in plants deficient in zinc can attract these parasites and, therefore, speed up the infection process (Streeter et al., 2001).

We still do not know the exact role played by zinc in relation to nematodes. However, supplying this mineral increased the activity of *Pseudomonas aeruginosa* IE-6S^{+} and *P. fluorescens* CHA0, helping in the biological control of *Meloidogyne javanica* (Treub) Chitwood (Siddiqui and Shaukat, 2002). Shaukat and Siddiqui (2003) reported that even when zinc alone was applied, it caused a decrease in the numbers of *M. javanica* and boosted increased growth in tomatoes. The authors also confirmed an increase in the antagonistic activity of rhizobacteria in the rhizobio group associated with the application of zinc. In another study, Siddiqui et al. (2002) confirmed that alterations in the soil when zinc was applied at 0.8 or 1.6 mg per kg^{-1} soil, whether alone or combined with *Pseudomonas aeruginosa* IE-6S^{+}, significantly reduced the penetration of *M. javanica* into tomato roots. At all nematode population densities, zinc reinforced the efficacy of the bacteria in reducing parasite penetration and subsequent development of galls. Absence of the bacteria and/or zinc increased the nematode population in the soil, causing a significant decrease in plant height, fresh weight and root protein content.

The increase in concentrations of antibiotics after applications of zinc could provide protection against diseases with a rapid onset, such as damping-off (*Pythium* and *Rhizoctonia* root rot), exceeding the bacterium's capability to take hold and becoming established in the rhizosphere, producing antibiotics *in situ* (Duffy and Défago, 1995). Zinc is known to stimulate antimicrobial polypeptide biosynthesis by biocontrol bacteria, change the structure of microbial communities and alter the physiology of plants, and can be used advantageously in controlling nematodes (Behal and Hunter, 1995; Siddiqui and Shaukat, 2002; Shaukat and Siddiqui, 2003).

Manganese (Mn) activates a number of enzymes on the chemical acid and subsequent pathways, leading to the biosynthesis of aromatic amino acids such as tyrosine and a number of other secondary compounds such as lignin and flavenoids (Barker and Pilbeam, 2007). For example, Mn^{+2} affects the PAL enzyme and stimulates peroxidases necessary for lignin biosynthesis. The lower lignin content in plants deficient in manganese is an indication of the need for this element at a number of stages in lignin biosynthesis and the reduction in the amount of root material contributes to lower plant resistance to pathogen attack (Marschner, 1997). It has been reported that supplying manganese to barley did not alter the number of immature females of *Heterodera avenae* Wollenweber, but untreated plant growth was significantly impaired by comparison with the growth of plants treated with the nutrient (Wilhelm et al., 1985). The authors think that applying manganese may have offset a deficiency in the absorption of the nutrient, caused by nematode infection.

Copper (Cu) influences the formation and chemical composition of the cell walls. In deficient leaves, the proportion of α-cellulose increases and lignin content decreased by half in comparison to leaves adequately supplied with copper. This effect is even more marked in the sclerenchyma cells in the stem (Marschner, 1997). In plants with severe copper deficiency, the xylem vessels are also insufficiently lignified, but lignification responds rapidly to treatment with the nutrient (Barker and Pilbeam, 2007). Copper must be supplied via the leaves at the beginning of the rapid plant growth phase and at the onset of flowering in the majority of cultivated species (Fancelli, 2008). According to Marschner (1997), lignification is inhibited in tissue deficient in copper because two copper enzymes are involved in the lignin biosynthesis pathway: polyphenol oxidase, which catalyzes the oxidation of phenolic compound lignin precursors, and diamine peroxide, which supplies the H_2O_2 necessary for oxidation by peroxidases. Tissues

deficient in copper therefore exhibit lower activity of these enzymes, accumulating phenolic compounds.

Fancelli (2008) points out that the most important micronutrients for preventing disease and that are usually ignored in production systems are Cu, B and Mn, since they play a fundamental role in the chemical acid pathway, the main plant defense pathway. It is also worth noting that, although Zn is the micronutrient most often taken into account in fertilizing programs, if Zn is supplied in high doses with no defined technical criterion, it can interfere with the use and metabolization of other nutrients, as well as encouraging the growth of fungi and fungal metabolite (micotoxin) production.

Boric acid is capable of forming complexes with diols and polyols, particularly with *cis*-diols. Polyhydroxyl compounds with a *cis*-diol configuration are necessary for forming these complexes. They include a number of sugars and their derivatives, and especially mannitol. These compounds serve as constituents of the hemicellulose fraction of the cell wall (Marschner, 1997). Some *o*-diphenols, such as caffeic acid and hydroxyferulic acid, are important precursors in the biosynthesis of lignin in the dicotyledons, because they have a *cis*-diol configuration and form stable borate complexes.

Boron deficiency is associated with morphological alterations and changes in tissue differentiation (Barker and Pilbeam, 2007). The formation of borate complexes with certain phenols is probably involved in the regulation of phenol levels and the synthesis rate for alcoholic phenols as precursors of lignin biosynthesis. Where there is a boron deficiency, phenols accumulate and polyphenol oxidase activity increases (Marschner, 1997). Depending on its dynamic in the soil and plant, boron should be supplied through the soil at the pre-sowing (or sowing) stage, using sources of medium solubility (Fancelli, 2008).

The balanced application of macro and micronutrients to the soil is the best way of ensuring that the crop is able to withstand the damage caused by nematodes. It is unlikely that fertilizing alone will control parasites of this kind. Therefore, fertilizers should be used initially to feed the plant, and be integrated with more effective methods of control (Ferraz et al., 2010).

It is worth pointing out that, in addition to studies aimed at evaluating the effects of plant nutrition on the nematode population, some researchers have been seeking answers using the opposite approach, i.e. the effect of nematodes on plant nutrition (Heffes et al., 1992; Hurchanik et al., 2004). Hurchanik et al. (2004) observed that coffee plantation infection by *Meloidogyne konaensis* Eisenback, Bernard and Schmitt significantly reduced the absorption of manganese and copper by the root system. Reductions in calcium and manganese were also observed, and attributed to root system damage caused by nematodes.

Heffes et al. (1992) evaluated the effect of *M. incognita* and *R. reniformis* on growth and nutrient contents in caupi beans and maize and observed that for each parasite-host combination there were major differences in root and aerial part nutrient concentrations when infected and uninfected plants were compared. Where the host was affected by the parasite, potassium concentrations were always lower and aluminum and vanadium concentrations always higher in the infected plants. In contrast, nematode infection resulted in a greatest decrease in iron concentration in the roots and aerial part. Although, nematode reproduction was higher in caupi beans than in maize, nutrient absorption through the roots was not affected, whereas in maize the absorption of nutrients was severely impaired. Nutrient translocation does not seem to be a limiting factor in host growth, since few differences were observed between the root/aerial part nutrient ratios of infected and uninfected plants. Other factors over and above nutrient absorption and translocation could be involved in the adverse effects of nematode parasitism in caupi beans, including water absorption, carbohydrate partitioning and phytoalexin toxicity.

In contrast, soybean plants parasitized by *H. glycines* exhibited yellowing and dwarfism as the main symptoms, which is why the disease is known as soybean yellow dwarf disease (Ferraz et al., 2010). This symptomatological situation is the result of nitrogen deficiency, stemming from a drastic drop in the nodulation of the symbiont bacterium *Bradyrhizobium japonicum* (Kirchner) Jordan (Andrade and Ponte, 1999). In many cases, the deficiency symptoms are common even if nutrients are available in the soil (Hurchanik et al., 2003), showing the dysfunction that occurs due to nematode infection of the root system.

Conclusions

There are still few studies on the influence of mineral nutrition on diseases caused by nematodes and some of the existing studies do not elucidate the mechanisms by which the nutrients reduce the phytoparasite population. In some nematode-plant interactions, the accumulation of cellulose, lignin and other elements brought about by plant nutrition confer nematode-resistance on the host. Some nutrients, such as silicon, seem to be directly related to the resistance induction process. This is, sometimes, accompanied by indirect responses, such increased activity of natural enemies. However, there are many contradictory results and numerous processes for which we still have no answers. In view of this, there is a need for conclusive research in order to elucidate the ways in which nutrients combat phytonematode infection.

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