

Research Progress on Manganese Toxicity and Revision Measures on Acid Soil

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Abstract

Manganese is a plant essential trace element, but excessive manganese will produce toxic effects on plants. There has attracted more and more attention on manganese toxicity as the main limiting factor for plant growth on acid soils. Research on effectiveness of soil manganese, plant manganese symptoms, manganese toxicity physical processes, Mechanisms of plants resistant manganese and corresponding measures of manganese toxicity management in recent years were reviewed in this study.

Keywords

Manganese; tolerance mechanisms; revision measures; research progress.

1. Introduction

Manganese is one of the essential microelements for plants. The minimum requirement of manganese for normal growth and development of plants is 30 mg·kg⁻¹dw [1]. However, when the manganese concentration in plants exceeds the critical value, chlorophyll synthesis and photosynthesis are inhibited, accompanied by the typical symptoms of manganese toxicity such as yellowing and shrinkage of leaves and brown manganese oxidation spots[2]. The excessive accumulation of manganese, on the one hand, interferes the absorption, transportation and utilization of other nutrient elements such as magnesium, iron, calcium, phosphorus, etc., leading to the imbalance of mineral nutrition[3]. on the other hand, it causes the abnormal reaction of cell antioxidant system, leading to the burst of free oxygen, destroying the normal structure of biofilm and chlorophyll, affecting the normal process of photosynthesis and other life processes[4]. In addition, excessive manganese can also increase the activity of IAA oxidase, accelerate the oxidation and decomposition of IAA, lead to the destruction of hormone balance in plants, and accelerate the senescence of plants[5].

The toxicity of manganese to plants mainly occurs in acid soil. When the pH value of soil is lower (< 5.5) or the redox potential (EH value) is lower (< 560mv), a large amount of manganese enters into the soil in the form of Mn²⁺, and the content of soil active manganese increases or decreases greatly and accumulates in the plant body, causing toxicity to the plant[6]. Manganese toxicity has become the second largest plant growth limiting factor in acid soil after aluminum toxicity[7]. Industrial acid precipitation, physiological acid or chemical acid fertilizer are increasing the process of soil acidification. Therefore, it is urgent to take effective measures

to prevent the existing manganese in the soil from poisoning the plants while restraining the acid expansion of the soil.

2. Manganese Toxicity of Plants on Acid Soil

2.1. Form and Availability of Manganese in Soil

The main forms of manganese in soil are as follows[8]: organic manganese, mineral manganese and inorganic salt containing manganese, water-soluble manganese and exchangeable manganese. The effective manganese for plants can be divided into three types: water-soluble manganese, exchangeable manganese and reducible manganese. The first two forms of manganese exist in the state of Mn^{2+} , while the latter is the part of manganese oxide with high valence which is easy to be reduced into effective Mn^{2+} , and the sum of the three is called active manganese. Generally, active manganese is used as the indicator of available manganese in soil. Some people think that not all of the easily reducible manganese is effective for plants, and the effective part only accounts for about 1/20[9].

The various forms of manganese in soil can be transformed into each other. The activity of manganese in soil is affected by the physical and chemical properties of soil pH, eh, humidity, organic matter and soil aeration, among which the most direct ones are pH and eh [9]. pH 6-6.5 is the critical value of manganese oxidation-reduction. pH<6 is favorable for Mn reduction, and pH>6.5 is favorable for Mn oxidation; meanwhile, when eh<500mv in soil, high valence Mn will be reduced to Mn^{2+} , increasing the activity of manganese[10]. Oloma [11] believed that the conversion of insoluble manganese to soluble manganese at pH 6-8 was related to pH value and eh value, but when pH value was 5 or lower, the influence of EH value was covered by the influence of pH value and became less obvious.

2.2. Symptoms of Plant Manganese Toxicity

Because of the different plant species, nutritional status and soil environment, the toxicity of manganese is different. The degree of manganese toxicity is also related to leaf age, distribution and concentration of manganese[12]. However, in general, the effect of Mn toxicity on the lower part is greater than that on the root system. Leaves are the target organs of Mn toxicity. 87% - 95% of Mn absorbed by plants is transferred to the upper part[13]. The typical symptoms of manganese toxicity are first manifested in mature leaves, Brown "manganese spots" formed by the combination of manganese oxide and phenolics materials at the edge, tip and vein of leaves[14]. With the accumulation of manganese, chlorophyll of new leaves decomposes, chloroplasts are destroyed, discolored patches appear, and further develop into vein chlorosis, yellowing, bleaching and withering similar to iron deficiency[15]. Manganese poisoning symptoms can be observed in many plants, but it is difficult to find a very typical specific manganese poisoning symptom at present. Generally, chlorophyll content, biomass, leaf iron activity, total iron/manganese and antioxidant system reaction are reported as evaluation indexes of manganese toxicity.

2.3. Physiological and Biochemical Process of Manganese Poisoning Plants

2.3.1. Manganese Toxicity and Plant Photosynthesis

Manganese participates in the composition of chloroplast, maintains the normal structure of chloroplast membrane, participates in the oxidation-reduction process of photosynthetic electron transport system and the photodegradation of water in the light system, and is one of the indispensable elements of photosynthesis[16]. However, excessive manganese can also lead to the decomposition of chlorophyll, destroy the structure of chloroplast, and hinder the normal process of photosynthesis[17].

Transmission electron microscopy showed that after a certain concentration of Mn treatment of *Euglena gracilis* for a certain period of time, most (nearly 90%) chloroplasts split and the shape was folded into a ribbon shape by a typical "cigar" shape. At the same time, the height of the chloroplast was The ordered thylakoid structure disintegrates into irregularly distributed thylakoid membrane fragments; the chlorophyll content is significantly reduced, especially the ratio of chlorophyll a/b is significantly reduced, indicating that excess manganese can destroy the normal structure of the chloroplast and seriously interfere with chlorophyll[18]. Experiments of *Solanum nigrum* L. and *S. chinensis* showed that the chlorophyll content decreased significantly under Mn stress, which reduced the photon quantum captured and transmitted to the PS reaction center, blocked the photosynthetic original reaction, and inhibited the electron transport process and electron transport rate: as the Mn concentration increased, Maximum photochemical quantum yield (F_v/F_m) maximum fluorescence (F_m) simultaneous photosynthetic quantum yield (Yield) and apparent electron transfer rate (ETR) decreased sharply, initial fluorescence (F_o) non-photochemical fluorescence quenching coefficient (NPQ) Significantly elevated - photosynthesis is significantly inhibited by manganese poisoning[19].

2.3.2. Manganese Toxicity and Enzyme Activation

According to statistics, manganese is the component of three enzymes and the activator of up to 36 enzymes, mainly involving phosphorylation, decarboxylation, reduction and hydrolysis[20]. At present, the most studied is the effect of manganese on the enzyme activity of plant antioxidant system. Manganese is one of the important redox agents in plants. Its in vivo reaction can directly regulate the concentration of Fe^{2+} in cells and the redox state of small molecule antioxidants such as ascorbic acid and glutathione. The chlorophyll can be photoactivated by chlorophyll in chloroplasts. Mn^{3+} , the oxidation-reduction potential is increased, causing the accumulation of reactive oxygen species (ROS) radicals such as $O_2^{\cdot-}$, H_2O_2 and $\cdot OH$, and the activities of antioxidant enzymes such as SOD, CAT and POD are affected, and the oxygen free radicals cannot be timely. Removal, resulting in membrane lipid peroxidation, the production of large amounts of malondialdehyde further deprives protein macromolecules and enzyme function[21-22]. In addition, manganese toxicity reduced the content and activity of enzymes (such as Rubisco, RA, RBP and GOGAT) related to CO_2 fixation and NH_4^+ absorption and reabsorption[23].

2.3.3. Manganese Toxicity and other Mineral Nutrition

The existence of excess manganese not only affects the absorption of N, P, CA, Mg and other mineral nutrients, but also interferes with the normal life function of related elements. The radius of Mn^{2+} is between Ca^{2+} and Mg^{2+} and close to Fe^{2+} , which may have the same binding site with Mg^{2+} , Ca^{2+} and Fe^{2+} in the plant root. Excessive manganese can inhibit the absorption of necessary elements magnesium, calcium and iron[24]. In addition, Mn^{2+} may replace Ca^{2+} and Mg^{2+} and interfere with the normal physiological function by combining with calmodulin, enzymes, chlorophyll and other biological macromolecules[25].

Among them, the influence of excess manganese on iron is more important. Most of the standard redox potentials of manganese system are higher than that of iron, so manganese can exist stably in the soil solution, while iron can hardly exist[26]. In addition, manganese has a strong antagonistic effect on iron. If the content of manganese is too high, it will promote the oxidation of iron and inhibit the reduction of iron, so that the soil iron mainly exists in Fe^{3+} with low activity[27]. At the same time, excessive manganese will accelerate the oxidation process of iron in vivo, and transform Fe^{2+} with physiological activity into Fe^{3+} without physiological activity, so as to reduce the amount of active iron when the total amount of iron in vivo is unchanged; on the other hand, because the chemical properties of Mn^{2+} and Fe^{2+} are similar,

high concentration of Mn^{2+} in vivo takes up the role of Fe^{2+} , sometimes resulting in physiological iron deficiency in plants[28].

3. Mechanism of Manganese Tolerance in Plants

The tolerance degree of plants to manganese toxicity is relative. Because of different manganese concentration, different plant species, different soil environment, the tolerance is also different. At present, the mechanism of manganese tolerance/accumulation in plants includes regionalization, chelation of organic acids, limiting absorption and efflux, antioxidation and ion interaction[17].

3.1. Regionalization

It is one of the important mechanisms for plants to improve the tolerance / accumulation of heavy metals that toxic metal ions are transported and stored in specific areas of tissues, organs or cells, and to reduce the concentration of metal ions in the metabolic active areas. Xu Xianghua and others believed that the leaves of Shanglu were the main organs of manganese accumulation, and the edge and epidermis of leaves were the main tissues of manganese accumulation and detoxification[29]. The results showed that vacuole was the storage site of excess manganese[30]. In addition, *Polygonum hydropiper*, a plant with manganese hyperaccumulation, is detoxified by combining root cell wall nodes[31].

3.2. Limiting Absorption and Efflux

Plants can oxidize Mn^{2+} to non effective state, thus limiting the absorption and transport of excessive Mn^{2+} . Under waterlogging conditions, the rice roots can oxidize Mn^{2+} into non effective tetravalent manganese compounds, forming a visible red iron manganese oxide film on the root surface, thus limiting the absorption[32]. The root of *Lupinus japonicus* can exclude manganese from the body by some mechanism, while hornbeam can detoxify it by secreting manganese phenol chelate from leaf epidermis[33-34].

3.3. Forming Metal Chelates

It is one of the important mechanisms of detoxification and tolerance of heavy metals in plants that metals in cytoplasm combine with ligands with high affinity to form chelates. Potential ligands include amino acids, organic acids, PCs and MMTS[35]. Bidwell et al. Found that there are a large number of organic acids in the leaves of manganese tolerant plants, such as oxalic acid, succinic acid, malic acid, malonic acid and so on, which can combine with free form manganese ions to form chelate, thus reducing the number of free manganese ions and reducing the toxicity of manganese to the body[36].

3.4. Antioxidant System

The membrane lipid peroxidation caused by excessive manganese is an important pathway of manganese toxicity. Therefore, it is also a major mechanism of manganese tolerance of plants to have strong antioxidant capacity. Zhang Yuxiu et al. Proposed that the strong antioxidant capacity of antioxidant enzymes is one of the Mn tolerance mechanisms of *Phytolacca*. *Phytolacca*, a heavy metal accumulating plant[37]; the high concentration of non protein sulfhydryl substances and ascorbic acid and other small molecule antioxidant substances maintained by the manganese tolerant plants can not only directly participate in the removal of active oxygen induced by manganese toxicity, but also be used as the synthesis precursor of Mn^{2+} chelating agents such as oxalic acid[38].

3.5. Ion Interaction

Under the condition of low pH, the increase of P can significantly reduce the toxicity of Mn to plants[39]. Calcium has an antagonistic effect on the absorption and accumulation of

manganese in plants, which can effectively reduce the phytotoxicity of manganese[40]. Iron and manganese also showed obvious antagonistic effect, excessive Mn affected the absorption and activity of Fe content, leading to physiological iron deficiency of plants; similarly, the increase of iron can also significantly reduce the absorption and transport of manganese by plants[24].

4. Correction and Prevention of Manganese Poisoning

With the aggravation of soil acidification, manganese toxicity in acid soil has become more and more serious, which seriously threatens the growth and yield of sugarcane and other crops[41]. It has become an urgent task to take appropriate agronomic measures to regulate the activity of manganese in acid soil and reduce the toxicity of manganese to plants.

4.1. Lime Application and Manganese Toxicity

The manganese in the soil is in a state of dynamic equilibrium. The proportion of manganese in the various forms varies with the pH value. The substitution and organic manganese decrease with the increase of pH value, oxidation state and amorphous iron. The bound manganese and the crystalline iron bound manganese increased with the increase of pH value, and the fierce bioavailability in the soil decreased significantly with the increase of pH value[42]. Therefore, raising the pH value of the soil is the primary measure to correct and control manganese toxicity. Lime can significantly reduce the active acid concentration and potential acid activity of soil, passivate metal ions such as Al and Mn, and improve soil fertility[43]. The application of lime has been proved to be an effective way to correct manganese toxicity in acid soil. On the one hand, lime increases the pH value of soil, which leads to the passivation of available manganese in soil; on the other hand, due to the similar nature of Ca^{2+} and Mn^{2+} ion radius and charge number, the absorption and accumulation of calcium on plant manganese is antagonistic, which effectively reduces the phytotoxicity of manganese[40].

4.2. Silicon Fertilizer and Manganese Toxicity

In response to the role of silicon in mitigating manganese, domestic and foreign scholars have conducted a lot of research and reported some possible mechanisms. In summary, there are mainly: silicon increases the oxidizing ability of the root system, thereby reducing the absorption of manganese[44]. Silicon promotes the distribution of manganese in the micro-domain of plant leaves more uniformly, reducing the relative manganese concentration of sensitive parts below its toxic concentration, thereby increasing the tolerance of plant leaf tissue to excess manganese[45]. The addition of silicon in the tissue inhibits the increase in peroxidase activity induced by manganese toxicity, and thus Si may act to maintain separation of cell walls, prevent peroxidase from entering, and contact with precursors of the brown matrix[46]. In vivo silicon and manganese accumulate in a metabolically inactive form near the hair follicles of the leaf surface to reduce manganese activity[47]. Silicon can effectively alleviate the oxidative stress caused by manganese toxicity and reduce the damage to membrane lipids and chlorophyll[48]. Silicon can increase the thickness of the epidermal cell layer of corn leaves, increase the partition storage capacity of manganese, and improve manganese tolerance[49]. In addition, Iwasaki et al. believe that the key part of silicon manganese poisoning is in the apoplast. On the one hand, the supply of silicon improves the ability of the cell wall to bind manganese, which increases the amount of manganese adsorbed by the cell wall, thereby reducing the amount of manganese entering the protoplast. On the other hand, water-soluble Si in the apoplast can directly bind Mn^{2+} and attenuate the toxicity of manganese in the apoplast[50].

4.3. Calcium Magnesium Phosphate and Manganese Toxicity

Calcium magnesium phosphate fertilizer has complex components, because it contains 12-14% P_2O_5 , 25-30% CaO , 5% Mg and up to 40% SiO_2 , it can increase the supply of P and Mg , at the same time, it has the soil modification effect of lime and silicon fertilizer. Pot experiments showed that the application of Ca , Mg and P could effectively improve the pH value of acid soil, the root activity and the soil fertility in the root zone, and the chlorophyll content in leaves and the biomass of plants[51].

4.4. Organic Fertilizer and Manganese Toxicity

The application of organic fertilizer is often used as a measure to control and improve soil heavy metal pollution. On the one hand, organic fertilizer can increase soil fertility and increase soil humus content, while manganese combined with humus is more difficult to decompose due to humus and has higher stability[52]. On the other hand, organic fertilizer can also reduce the bioavailability of heavy metals in the soil and reduce the absorption of heavy metals by crops[53]. The application of organic fertilizer and humic acid can adjust soil porosity, improve pH value and field water holding capacity, effectively improve the physical and chemical properties of acid soil series in the southern clay heavy red soil, improve soil fertility and alleviate heavy metal toxicity[54].

In addition, the use of foliar spray iron fertilizer and growth is also an effective way to correct manganese poisoning. Foliar application of iron fertilizer directly increased the active iron content of the leaves, provided Fe/Mn value, relieved the physiological iron deficiency of plant leaf cells, and significantly reduced the absorption and transport of manganese by roots[55]. The supplement of exogenous IAA can increase the level of leaf tissue auxin, rebuild the hormone balance caused by the increase of IAA oxidase caused by manganese toxicity, and inhibit the aging process such as chlorophyll decomposition and membrane peroxidation[56].

5. Discussion and Prospect of Manganese Toxicity in Acid Soil

1) The research on manganese toxicity in acid soil mainly focuses on indoor experiments, but less on outdoor sites. The outdoor site is affected by many factors, and the indoor experimental environment conditions are easy to control, so the environmental conditions of the two are quite different. There are still many problems to be solved in the application of research on the remediation of manganese toxicity in acid soil to outdoor sites.

2) Due to the current situation of manganese mining and extensive agricultural measures, the problems of soil acidification and plant manganese toxicity are more and more prominent. There have been a lot of researches on the control of manganese toxicity in soil, but the emphasis is not strong from the perspective of prevention and the implementation of agricultural improvement measures such as fallow rotation. Therefore, it may be one of the research directions in the future to make good use of the existing research basis, supplemented by the establishment of soil manganese toxicity model and soil manganese toxicity evaluation system in different areas to prevent pollution.

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