Trends in Plant Science

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Review

Manganese Deficiency in Plants: The Impact on Photosystem II

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Manganese (Mn) is an essential plant micronutrient with an indispensable function as a catalyst in the oxygen-evolving complex (OEC) of photosystem II (PSII). Even so, Mn deficiency frequently occurs without visual leaf symptoms, thereby masking the distribution and dimension of the problem restricting crop productivity in many places of the world. Hence, timely alleviation of latent Mn deficiency is a challenge in promoting plant growth and quality. We describe here the key mechanisms of Mn deficiency in plants by focusing on the impact of Mn on PSII stability and functionality. We also address the mechanisms underlying the differential tolerance towards Mn deficiency observed among plant genotypes, which enable Mn-efficient plants to grow on marginal land with poor Mn availability.

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Mn deficiency often occurs as a latent disorder without any growth restrictions or clear leaf symptoms, despite significant disintegration of PSII under these conditions.

Photosystem II is the primary target of Mn deficiency in plants.

Mn deficiency leads to destabilization of PSII super- and subcomplexes.

ICP-MS based analysis of metal binding in photosystem complexes provides a valuable tool to study the loading and internal use of Mn and other biometals required for efficient photosynthesis.

Traditional cereal landraces constitute a valuable germplasm for reintroducing genotypic diversity to improve nutrient efficiency and increase crop robustness.

Photosynthesis Is a Key Target of Mn Deficiency

Plant health and plant vigor is of fundamental importance to agricultural productivity. Constantly changing environmental conditions means that plants must cope with fluctuations in light intensity and spectral composition, as well as variations in water and nutrient availability. For this reason, plant productivity greatly depends on a series of processes that influence and modulate the photosynthetic machinery [1,2].

Adequate supplies of the essential plant nutrients are required for optimal plant growth. Importantly, the nutrient supply must be balanced because deficiency in any essential nutrient cannot be compensated for by any other nutrients – as stated by the classical Liebig law of the minimum. Nutrient deficiency therefore restricts plant growth and eventually harvest yields [3,4]. In the photosynthetic electron transport processes, several metals act as cofactors and catalysts [5]. Plants have an essential dependence on Mn owing to its indispensable role in the OEC of PSII [6,7]. Accordingly, Mn deficiency has detrimental effects on the photosynthetic apparatus owing to reduced photosynthetic electron transport and oxidative stress.

As an inherent consequence of any nutrient limitation, plants utilize other natural resources less efficiently [8]. In terms of Mn this concerns reduced water use efficiency and decreased root functionality leading to the suboptimal use of for example phosphorus, potentially leading to soil and water pollution. Thus, Mn represents a micronutrient with a wide-ranging impact on the efficient utilization of natural resources and on the sustainability of commercial plant production.

The Physiological Responses to Mn Deficiency

The amount of Mn^{2+} in the soil available to the plant is influenced by soil parameters such as pH, soil porosity, water content (redox potential), and microbial activity (Figure 1). Hence, plants

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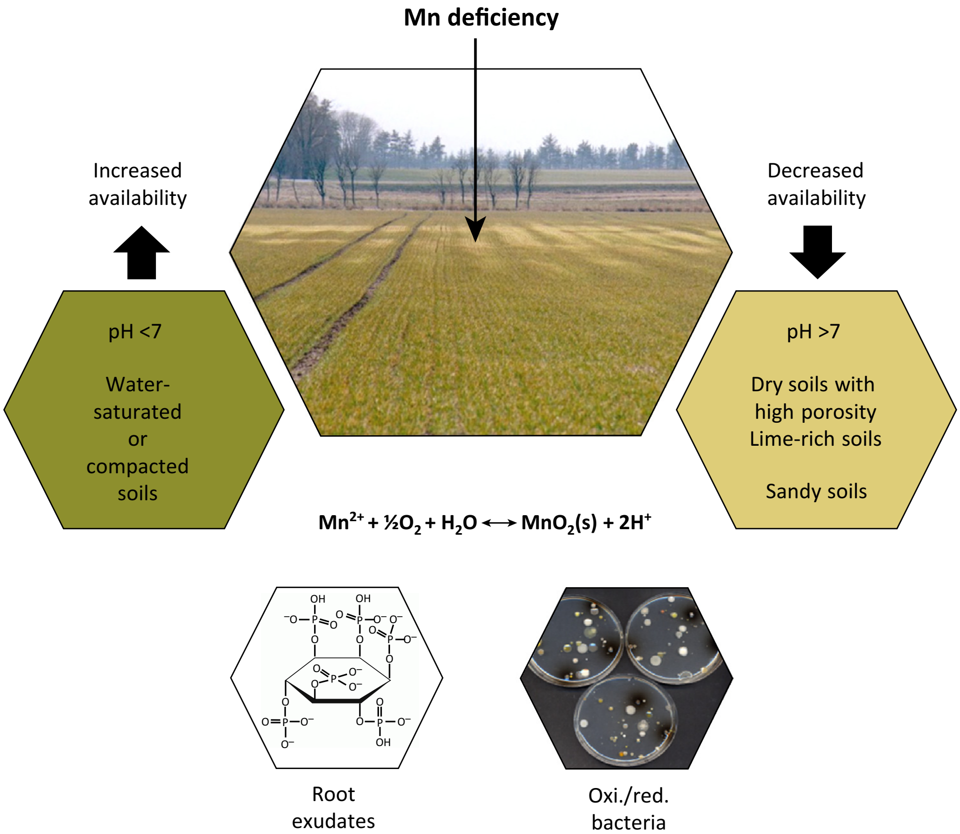

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Figure 1. The Key Parameters Controlling Plant Availability of Manganese (Mn) in Soils. It is rarely the total amount of Mn in soils which limits plant growth, but instead low concentrations of the plant-available form, Mn^{2+}, which is controlled by the chemical equilibrium displayed in the center of the figure above. From the equation, it is evident that plant-unavailable Mn oxides (MnO_2) are in equilibrium with plant-available Mn^{2+} ions, but with a stability constant log $K_{MnO_2} = 41.7$ the equilibrium is shifted far to the right, and typically the resulting Mn^{2+} concentrations in the soil solution are in the nM range. From the equilibrium it can be seen that lowering of pH and/or the oxygen tension of soil pores will increase plant-available Mn^{2+}. It can also be deduced that, for each reduction of pH by one unit, plant availability of Mn is increased by a factor of 100. In water-saturated soils or in compacted soil areas where the oxygen tension of soil pores is low (e.g., near tractor tracks), plant-available Mn is increased, as clearly illustrated in the photograph. For this reason, Mn deficiency-prone soils are often porous sandy soils or lime-rich soils with resulting high pH-values shifting the equilibrium to the right. Other factors influencing Mn availability include the ability of plants to establish symbiosis with soil microorganisms such as Mn-oxidizing (oxi.) and -reducing (red.) bacteria, and the release of root exudates (e.g., phytase and organic acids) to liberate Mn by enzymatic degradation of Mn phytate complexes, or by dissolution of inorganic Mn phosphates or carbonates to increase Mn availability in the rhizosphere. Photo by K.H. Laursen.

grown on calcareous soils with elevated pH, and on sandy soils with high porosity, are in particularly prone to Mn deficiency owing to conditions favoring oxidization of Mn to unavailable Mn oxides (Figure 1) [9]. Such soil types prone to Mn deficiency are prevalent in the northern part of Europe including Scandinavia [10–12] and the UK [13,14], are widespread in the northern parts of USA and Canada, and also in southern Australia [15], whereas their occurrence in Asia is less clear [16]. Overview of the exact distribution and incidence of Mn deficiency is almost impossible to obtain owing to the latency of deficiency symptoms.

Mn deficiency strongly affects photosynthesis; however, visual symptoms of diffuse and/or interveinal chlorosis (Figure 2), reflecting photochemical disturbances, are only visible when plant growth is severely depressed [17]. At the onset of Mn deficiency, the symptom stratification is