

Micronutrient Deficiency and Toxicity in Plants

Subjects: [Plant Sciences](#)

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Micronutrients are essential for plants. Their growth, productivity and reproduction are directly influenced by the supply of micronutrients. Currently, there are eight trace elements considered to be essential for higher plants: Fe, Zn, Mn, Cu, Ni, B, Mo, and Cl. Possibly, other essential elements could be discovered because of recent advances in nutrient solution culture techniques and in the commercial availability of highly sensitive analytical instrumentation for elemental analysis.

micronutrients

proteomics

genomics

nutrient toxicity

1. Introduction

Essential nutrients (macro and micro) are required by plants for appropriate functioning and development. The significance of micronutrients in plant nutrition is well recognized. Micronutrients comprise less than 1% of the dry weight of most plants and are vital for their growth [1]. Plant classified micronutrients include boron, chlorine, copper, iron, manganese, molybdenum, nickel and zinc, which are vital for completion of the plant's life cycle (Figure 1) [2]. They are also essential to maintain the stability of proteins and cellular structures. Through their interactions with other physiologically active molecules and enzymes, micronutrients play an essential role in the biosynthesis of proteins, nucleic acids, cofactors, carbohydrate metabolism, lipid metabolism, stress tolerance, chlorophyll maintenance, electron transport, anti-oxidative systems and much more. Hence access to micronutrients is critical for optimum crop nutrition and development (Figure 2) [3]. The bioavailability of micronutrients is heavily influenced by climatic factors like drought, severe rain, waterlogging or salinity [4]. Energy metabolism, primary and secondary metabolism, cell defense, gene expressions and regulations, hormone sensing, signal transduction, and reproduction are all influenced by micronutrients. The proportion of micronutrients in soil is determined by the geological substrate and pedogenesis management strategies. The ideal concentration of each micronutrient in the crop is influenced by chemical and physical features of the soil, such as soil pH, nutrient availability, clay minerals, microbial activity, amount of organic matter in the soil, quantity of other nutrients, and other factors that might affect micronutrient absorption and efficacy (Table 1). Although the fraction of micronutrients available in the soil may exceed a single plant's requirements, the accessible proportion may be insufficient for all, resulting in nutritional deficiency in the crop. In Indian soils, improper nutrient management leads to multi-nutrient deficits [5]. Growth of the plant is constrained either by lack of micronutrients, nutrient toxicity or soil conditions.

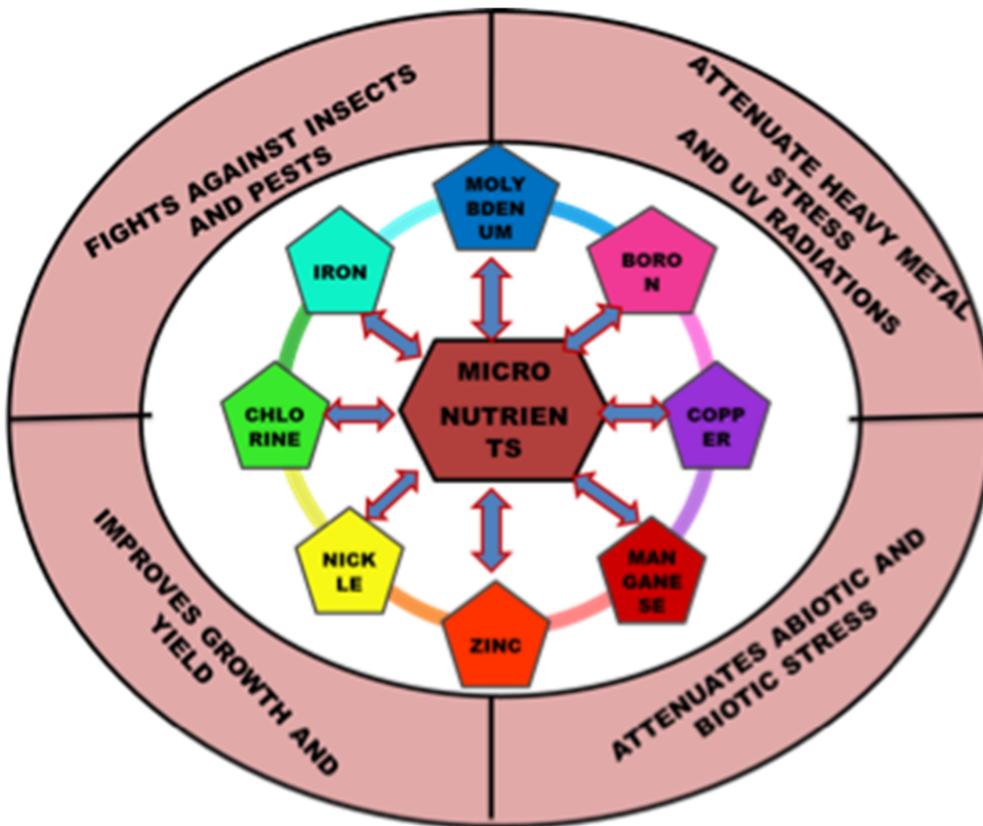


Figure 1. Versatile role of micronutrients in plant’s growth and development.

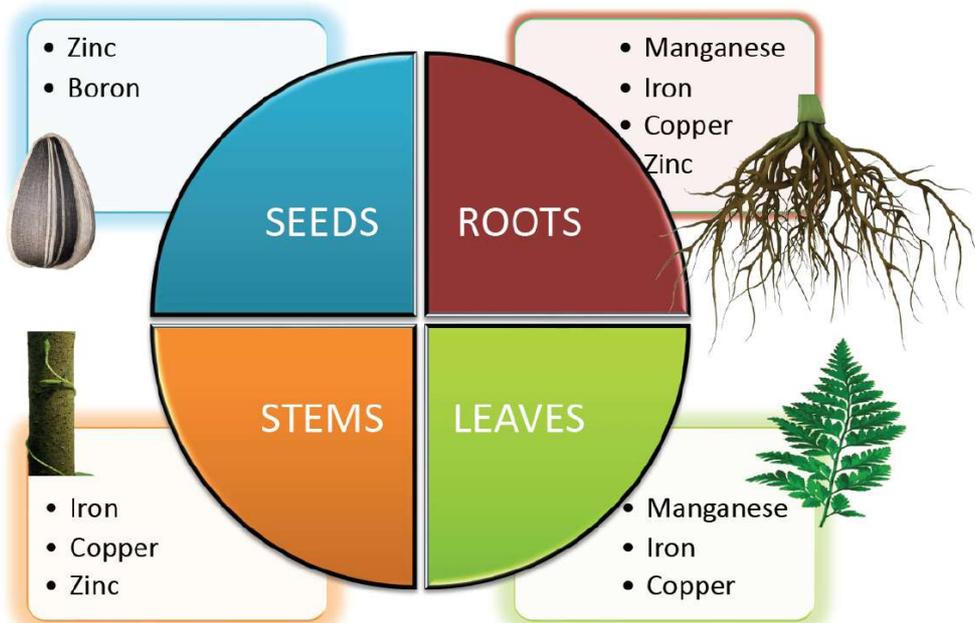


Figure 2. Micronutrients involved in the growth and development of different parts of the plant.

Table 1. Micronutrients, their modes of intake and their concentrations in the leaves.

S. No.	Micronutrient	Year of Discovery	Ionic Form of Intake	Normal Value (ppm)	Deficient Value (ppm)	Toxic Value (ppm)
1	Boron (B)	Warington (1937)	H_2BO_3 , $H_2BO_3^-$, HBO_3^{2-} , BO_3^{3-}	10–20	5–10	50–200
2	Chlorine (Cl)	Broyer et al. (1954)	Cl^-	100–500	Less than 100	500–1000
3	Copper (Cu)	Lipman and Mackinney (Sachs 1931)	Cu^{2+}	5–30	2–5	100–200
4	Iron (Fe)	Sachs (1860)	Fe^{2+} , Fe^{3+}	100–500	Less than 50	More than 500
5	Manganese (Mn)	Mchargue (1922)	Mn^{2+}	20–300	15–20	300–500
6	Molybdenum (Mo)	Arnon and Stout (1939)	MoO_4^{2-}	0.1–2.0	0.03–0.15	More than 100
7	Zinc (Zn)	Sommer and Lipman (1926)	Zn^{2+}	27–150	10–20	100–400

Micronutrient depletion develops in the soil as a result of farming techniques, such as intensive farming, monocultures, and acid soil liming, which affect the plants in various ways (Table 2, Figure 3). When nutrient demand exceeds the rate of supply, the plant frequently switches to alternative metabolic pathways, which are often dependent on limiting micronutrients. A decrease in one micronutrient content might reduce the bioavailability of other nutrients in the soil [6]. Although, in certain cases, plants seem unable to detect a deficit because micronutrient availability is impacted by organic matter content, soil pH, adsorptive surfaces, and other biological, chemical, and physical environmental conditions. Prolonged negligence of micronutrient supplementation and aversion of organic fertilizers are major contributors to micronutrient insufficiency and plants respond to these conditions in a variety of ways, by reprogramming transcriptional and translational modifications [2]. Identifying metal-tolerant genes and/or proteins is the first step in deciphering the pathways linked with micronutrient stress tolerance [4].

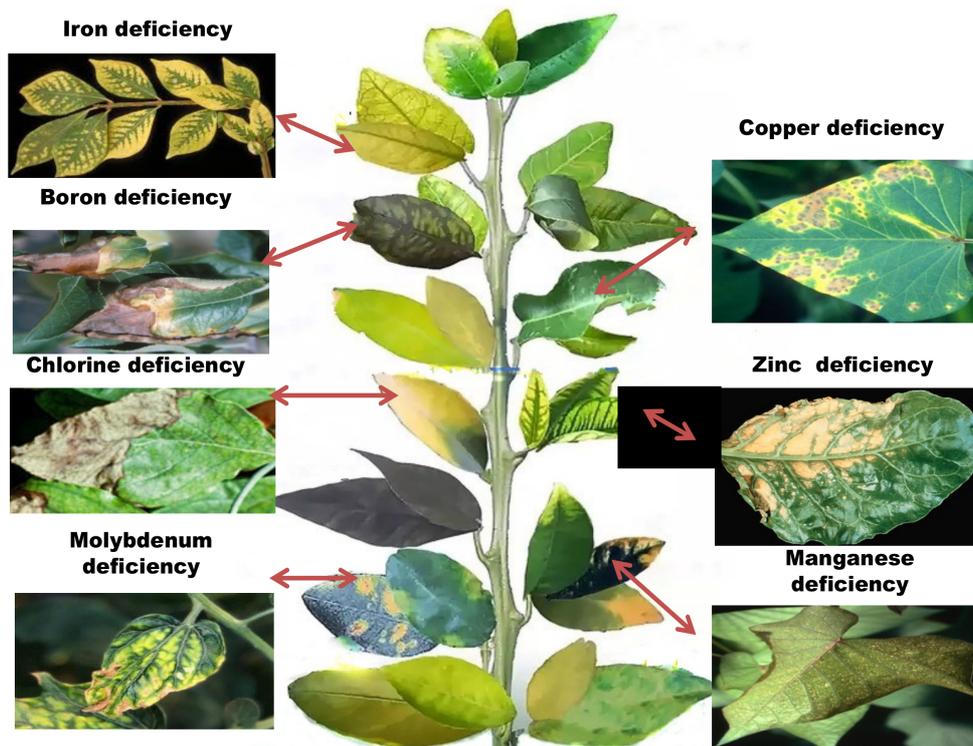


Figure 3. Symptoms of micronutrient deficiencies in plants.

Table 2. Summary of micronutrient functions and deficiency symptoms.

S.No.	Micronutrients	Representative Constituents/Proteins	Functions	Symptoms of Deficiency	Probable Cause of Deficiency & References Method of Correction
1	Zinc (Zn)	Cu–Zn superoxide, Peptide deformylase, enzyme carbonic anhydrase (CA), α-Mannosidase, Matrix metalloproteinase alcoholic dehydrogenase, and superoxide dismutase (SOD)	role in nitrogen metabolism and photosynthesis, controls the concentration of auxin in plants, increases seed viability and seedling vigor, protection against abiotic and biotic stresses	Reduced vigor, chlorotic leaves, white streaks parallel to leaf blade, slow growth, restricted RNA and protein synthesis	Low Zn in soil, high soil pH— lower soil pH, apply foliar spray or add Zn to soil. [8] [9] [10] [11] [12] [13] [14] [15] [16]
2	Copper (Cu)	Plastocyanin Cu-Znsuperoxide, Ascorbate, Cu-metallothionein, biosynthesis oxidase,	saves plants from diseases, improves the fertility of male flower,	Leaf tips dries, break down and dies, ragged leaves, reduced growth	Low soil Cu, high organic matter— apply foliar [17] [18] [19] [20] [21] [22] [23] [24] [25] [26]

S.No.	Micronutrients	Representative Constituents/Proteins	Functions	Symptoms of Deficiency	Probable Cause of Deficiency & References Method of Correction
		Mo-cofactor, dismutase, polyphenol or catechol oxidase, tyrosinase, laccase, Cytochrome-C oxidase, Ethylene receptor ascorbic oxidase and Polyphenol oxidase	concerned with the oxidation of iron in plants		spray or add Cu to soil
3	Iron (Fe)	Aconitase, dismutase, Xanthine dehydrogenase, Ferredoxin, porphyrin NADH, Succinate, Leg hemoglobin, heme and heme enzymes peroxidase oxidase, dehydrogenase, Nitrate reductase oxidoreductases, Thioredoxin reductase, Cytochrome P450, Aldehyde oxidase, Catalase, Nitrite reductase, Lipoxygenase, Alternative oxidase, Fe-superoxide Ferritin and other functional metallic proteins	Present in haemoglobin of the leguminous root nodules, leg-haemoglobin and is involved in nitrogen fixation as a constituent of ferredoxin	Interveinal, creamy chlorosis on apical leaves, stunted shoots, reduced yield	Waterlogged soil, over fertilized, excess of elements like Mn— spraying plant with iron rich fertilizer, chelated iron powder or blood meal directly to the soil [27] [28] [29] [30] [31] [32] [33] [34] [35] [36] [37] [38] [39] [40] [41] [42] [43] [44] [45] [46]
4	Manganese (Mn)	Malic enzyme, Mn-superoxide, amidohydrolase, primary component of water-splitting enzyme related to photosystem II, PEP carboxylase, Allantoate, Iso-citrate lyase, dismutase PEP-carboxykinase	Involved in tricarboxylic acid cycle in oxidation and reduction reactions, activates several enzymes such as oxidoreductases, hydrolases and lyase, also autocatalyzes isocitrate dehydrogenase, malic	Reduced quality and yield, stunted plants, intervenial chlorosis in leaves, yellow cast in deficient areas. Death of basal leaves, decreased cold hardiness, growth of lateral roots stopped, inhibition of nitrate metabolism.	Low soil Mn, high soil pH due to over liming— lower soil pH, apply foliar spray or add Mn to soil [47] [48] [49] [50] [51] [52]

S.No.	Micronutrients	Representative Constituents/Proteins	Functions	Symptoms of Deficiency	Probable Cause of Deficiency & References	Method of Correction
			dehydrogenase, glycoaminase and D-alanyl synthase.			
5	Boron (B)	Rhamnogalacturonan II	increases cell wall thickness and flower production, as well as retention, pollen tube elongation and germination, along with seed and fruit development. It also helps in the translocation of photosynthates. It inhibits IAA oxidation and gives drought tolerance to crops	Thick and leathery old leaves, shoot tip death, rosette leaves with short internodes, excess branching, short, twisted and/or ruptured petioles, vegetables with hollow heart, small and deformed/no fruits with cork spots chlorosis, stubby roots, inhibited nitrogen metabolism.	Low soil B especially on sandy soils or light textured soils—apply foliar spray or add B to soil	[53][54][55][56]
6	Molybdenum (Mo)	nitrogenase, sulphite oxidase, nitrate reductase Aldehyde oxidase and xanthine oxidase/dehydrogenase	aids in the synthesis of ascorbic acid, formation of pollens and anthers, acts as a remedy to excessive copper, manganese and zinc	stunted growth with twisted stems, leaves turning pale green, necrotic area in leaves along the mid rib between veins and along leaf edges	Low soil pH, low Mo content in soil— inoculate seed with Mo, apply foliar spray or add Mo to soil	[33][34][57][58]
7	Chlorine (Cl)	Oxygen-evolving complex Seismonastic movement	activates enzymes that are involved in starch utilization which affects germination and energy transfer. Inmoisture-stress conditions	stunted/restricted growth, stubby roots, interveinal chlorosis, non-succulent tissue, wilting	Low soil Cl especially in soils subjected to leaching— apply Cl containing fertilizer	[55][59]

because they have developed systems to store these and utilize them for defensive functions (Figure 4).

3). When with the). Plants e field of ent efflux nutrients

S.No.	Micronutrients	Representative Constituents/Proteins	Functions	Symptoms of Deficiency	Probable Cause of Deficiency & References Method of Correction
			chlorine helps in the movement of water into cells and maintenance of that water. Chlorine also controls the opening and closing of stomata on leaf surfaces		

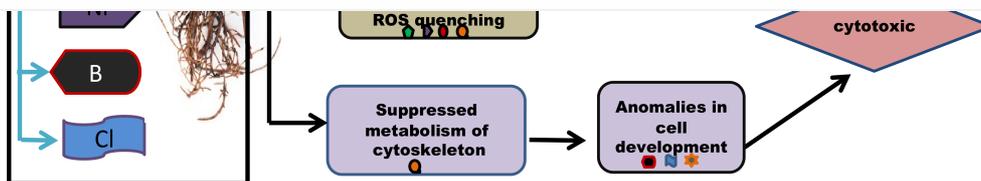


Figure 4. An outline presenting the molecular and the biochemical mechanisms involved in micronutrient cytotoxicity in plants.

Table 3. Micronutrient toxicity.

S. No.	Micronutrients	Type	Symptoms of Excess Usage	References
1	Zinc (Zn)	Metal	Inhibited root growth, young leaf chlorosis, interveinal mild chlorosis in young leaves starting from base and spread towards apex followed by reddish brown coloration, rolling of leaves	[61]
2	Copper (Cu)	Metal	Reduced vigor, inhibited root growth/root damage, older leaves develop orange or pink coloration followed by severe rolling of leaf margins due to loss in turgidity	
3	Iron (Fe)	Metal	Reduced yield, bronzing and stippling of leaves, and, in some plants, acid is secreted from the roots	
4	Manganese (Mn)	Metal	Tissue injury, leaf sheath and lower parts of stem in cereal normally consist of minute brown spots, legumes develop brown or purple spots over leaf margin, deficiency symptoms of other nutrients	
5	Boron (B)	Metalloid	Toxicity results in dark brown speckles or necrosis on the edge of older leaves, cupped and wrinkled young leaves	
6	Molybdenum (Mo)	Metal	Leaf malformation, tints of golden yellow or blue color in leaves	

S. No.	Micronutrients	Type	Symptoms of Excess Usage	References
7	Chlorine (Cl)	Non metal	Death of leaf margin, leaves are reduced in size and number, have bronze or yellow coloration with brown or scorched leaf margins.	

Metal	Plant Species	Plant Part	Extraction Method	Protein Name	Function	Regulation	References
Boron (B)	<i>Citrus grandis</i>	Root	iTRAQ	Alcohol dehydrogenase 1	Energy metabolism	Down	[62]
				Serine/arginine-rich 22	Nucleic acid metabolic process	Down	
				Clathrin light chain protein	Cellular cytoskeleton and transport	Up	
				Peroxiredoxin IIF	Cellular response to stress	Down	
				Phospholipase C2	Signal transduction	Down	
	<i>Arabidopsis thaliana</i>	Leaf	2-DE, LC-MS/MS	Rubisco activase	Photosynthesis	Up	[63]
				Actin 7	Metabolism	Down	
				Fructose-bisphosphate aldolase	Energy metabolism	Up	
				Glycolate oxidase	Photosynthesis	Down	
				Thymidine kinase	Protein translation and synthesis	Down	
Copper (Cu)	<i>Sorghum bicolor</i>	Leaf	2-DE, MALDI-TOF MS	Thaumatococin-like protein	Stress and defense	Up	[64]
				Maturase K	Growth and development	Down	
				Alcohol dehydrogenase	Oxidation–reduction process	Up	
	<i>Oryza sativa</i>	Root	2-DE, MALDI-TOF MS	Putative peroxidase	Anti-oxidation and detoxification	Up	[65]

Metal	Plant Species	Plant Part	Extraction Method	Protein Name	Function	Regulation	References	
Iron (Fe)				Putative cold shock protein-1	Transcriptional regulation	Up	[66]	
				Putative elongationfactor EF-2	Protein synthesis	Down		
				Glutamine synthetase shoot isozyme	Amino acid synthesis	Down		
	<i>Allium cepa</i>	Root	2-DE, MALDI-TOF MS	Glutaredoxin	Defense	Up		
				Ran-binding protein 1	Protein synthesis	Down		
				Cinnamoyl-Co-A-reductase 1	Cell wall synthesis	Down		
				Proliferation-associated 2 g4	Cell cycle and DNA replication	Up		
				Oxidoreductase	Hormone metabolism	Up		
				WAKL4, WAK-like receptor-like kinase	Signaling	Up		
	<i>Arabidopsis thaliana</i>	Root	Itraq, LC-MS	FRO3, ferric chelate reductase 3	Metal handling	Up		[67]
				SAPX, Stromal ascorbate peroxidase	Redox	Down		
				IRT3, Iron regulated transporter3	transport	Down		
	<i>Zea may</i>	Root	LC-MS/MS	Aquaporin PIP2-2	Transport proteins	Down		[68]
Gibberellin receptor GID1L2				Signaling proteins	Down			
Aldolase				Metabolism	Up			

Metal	Plant Species	Plant Part	Extraction Method	Protein Name	Function	Regulation	References
Manganese (Mn)	<i>Cucumis sativus</i>	Root	2-DE, ESI-LC-MS	Actin-2	Cytoskeleton	Down	[69]
				Callreticulin 2	Protein folding	Up	
				Phosphoglycerate kinase	Glycolysis	Up	
				Malate dehydrogenase	Carbohydrate-related metabolism	Up	
				Alanine aminotransferase	Nitrogen-related metabolism	Up	
				Xylan 1,4-beta-xylosidase	Metabolism of sucrose	Down	
				Acetohydroxyacid isomeroeductase	Protein metabolism	Down	
<i>Citrus grandis</i>	Root	2-DE, MALDI-TOF MS, LTQ-ESI-MS/MS	Maturase K	Nucleic acid metabolism	Up	[70]	
			Alcohol dehydrogenase	Carbohydrate metabolism	Up		
			Iron- sUperoxide dismutase	Stress response	Down		
			Valosin-				
Metals	Plant Species	Tissue	Method of Identification	Gene	Functions	Regulation	References
Boron (B)	<i>Arabidopsis thaliana</i>	Root	qRT-PCR	SHB1/HY1	B-tolerance	Up	[72]
				LOC_Os08g30740	ABC transporter	Down	
	<i>Oryza sativa</i>	Root	Microarray, qRT-PCR	LOC_Os10g30156	Starch synthase	Down	[73]
				LOC_Os10g30080	Xylosyltransferase	Down	
				Ciclev10017846m	Ubiquitin-protein ligase activity	Down	
	<i>Citrus sinensis</i>	Leaf	Illumina sequencing, qRT-PCR	Ciclev 10012377m	Transcription factor	Up	[74]
Ciclev 10009779 m				Blue copper protein	Up		
Zinc (Zn)	<i>Arabidopsis thaliana</i>	Whole plant	qRT-PCR	PDR8	Phytochelatin synthesis	Up	[75]

Metals	Plant Species	Tissue	Method of Identification	Gene	Functions	Regulation	References
				ABCCI	Metabolism	Down	
Iron (Fe)	<i>Citrus sinensis</i>	Whole plant	qRT-PCR	Cs3g19420	Ethylene-responsive transcription factor	Up	[76]
				Cs4g12540	Ethylene synthesis	Down	
				Cs9g02930	Flavone synthase	Down	
	<i>Arabidopsis thaliana</i>	Root	qRT-PCR	FRO2	Iron homeostasis	Up	[77]
Manganese (Mn)	<i>Arabidopsis thaliana</i>	Root	qRT-PCR and RNA sequencing	AT5G05960	Bifunctional inhibitor	Down	
				AT4G39940	Glucosinolate	Up	[78]
				AT1G15820	metabolism Photosynthesis	Up	
	<i>Citrus sinensis</i>	Leaf	cDNA-AFLP and qRT-PCR	TDF #065-1	Energy metabolism	Up	
				TDF #073-1	Cell transport	Down	[79]
				TDF #103-2	Stress responses	Down	
Copper (Cu)	<i>Arabidopsis thaliana</i>	Whole plant	qRT-PCR	OsLAC10	Laccase activity	Up	
				AtLAC11	Lignin biosynthesis	Up	[80]
	<i>Oryza sativa</i>	Whole plant	Western blotting, qRT-PCR	OshMA4	Copper accumulation [2]	Down	[74]

proteins and methods

2. Molecular Approaches for Understanding Micronutrient Stress Mechanisms in Plants

Micronutrient insufficiency and toxicity might be detected using both proteomic and genomic investigations [6]. The distribution of micronutrients all throughout the soil profile influences their availability to plants. Plants adapt dynamically to maintain nutrient supply and demand in the appropriate range. Proteomics is a popular molecular method for defining full proteomes at the organelle, cell, or tissue level. It is also helpful for comparing proteins under various adverse environmental conditions [81]. Sub-proteome analysis of nutrient deficit plants is also becoming popular, which includes analysis of apoplastic fluids, root plasma membrane, microsomal shoot fractions, phloem saps detergent-resistant membranes, thylakoid membranes and root hairs [82]. Proteins are the key molecules involved in several biochemical processes, and, as a result, a thorough understanding of stress induced genomic and proteomic changes aids in deeper understanding of the stress induced pathways. Changes in

proteomic expressions are correlated with changes in the gene, transcriptome and metabolism levels. However, alterations at the transcriptional level may not always correspond to changes at the proteomic level. Protein expression is regulated not just at the transcriptional level, but also at the translational and post-translational stages, despite the perception of reciprocity between mRNA and protein [83]. As a result, information gathered at the translational and post-translational levels can provide more insight into protein responses, their modifications and functional relationships than genome-based predictions can provide. As proteins act as direct mediators of response, examining these alterations at the proteome level is critical [84]. These variations are reflected in the proteome compositions, hence proteomic investigations might be useful in identifying important protein components. These could be used as possible biomarkers in the underlying process. Current proteomic investigations have mostly focused on detecting quantitative changes and have relied on comparative proteomic techniques that include two-dimensional gel electrophoresis (2-DE) followed by mass spectrometry analysis (MS). This should lead to a better knowledge of the interactions between various elements, as well as the plant's responses to environmental conditions at various phases of growth and development.

The genome of a life form is consistent, but the proteome is much more complex because protein expression changes with time and environmental factors [85]. Several researchers used transcriptome analysis to examine the expression patterns of genes in plants under heavy stress throughout the last decade. Gene expression at the mRNA level may be used to determine plant responses to a micronutrient buildup (**Table 5**) [86]. Furthermore, transcriptional analysis has some drawbacks, such as a lack of correlation between changes in mRNA expression and changes in their related proteins. By combining this method with genotyping technologies, researchers are able to quickly identify genes and networks that coordinate accumulation of elements in plants. A detailed summary of different genomic and proteomic studies carried out using different micronutrients is listed below.

2.1. Boron

Boron deficiency develops as a result of decreased root respiration, advanced cellular transport, rise in antioxidants and ROS-scavenging proteins [87]. Total proteins in boron deficit white lupin (*Lupinus albus*) root extracts were analyzed using 2D-PAGE, and 128 proteins were determined using mass spectrometry, all of which were involved in cell structure and metabolism, protein metabolism, energy pathways and defense mechanism [88]. ITRAQ study of the roots of *Citrus sinensis* seedlings subjected to Boron deficiency revealed a rise in level of 164 proteins, as well as reduction in level of 225 proteins [87]. Many of these proteins were involved in signal transduction, cell transport, stress responses, nucleic acid metabolism, protein metabolism, carbohydrate metabolism, biological regulation, lipid metabolism, cytoskeleton metabolism and energy metabolism.

Boron-toxicity-responsive proteins have been identified through MS analysis in research carried out on the leaves of *Citrus sinensis* and *Citrus grandis* (B- tolerant citrus species). Toxicity to boron is relatively common in alkaline and saline soils. Boron toxicity increases the amount of PSI type III CAB in barley leaves [89]. According to the 2D-PAGE research of boron toxicity-responsive proteome in oranges, it was hypothesized energy metabolism and photosynthesis might have resulted in increased CO₂ absorption and, hence, resulted in a better continuation of energy balance [90]. Proteins associated to ROS-scavengers were highly accumulated in Boron-toxic *C. grandis*

compared to *C. sinensis* to overcome oxidative stress, according to the analysis of root samples [91]. In a separate study, root systems of these citrus species were tested to study the toxicity of boron. In both species, there were 44 up- and 66 down-regulated genes, with Root Hair Defective 3 expressing in *C. sinensis* and villin4 being repressed. The discovery of boron-toxic-responsive genes involved in the lipid, nucleic acid and energy metabolisms helped researchers to further understand the mechanisms behind boron-toxicity in citrus species [92]. Using the SHB1/HY1 gene and increased levels of BOR4 expression, researchers established the boron homeostasis concept in Arabidopsis root samples [72]. According to the findings, excessive boron absorption in plants promotes excess transcription of the BOR4 gene, an efflux type boron transporter, encouraging the exclusion of excessive boron. In *Oryza sativa*, the genetic diversity linked with boron tolerance was investigated by looking at genes involved in biochemical binding, transport, transcriptional control, and redox homeostasis [73].

2.2. Chlorine

The majority of soils are not chlorine deficit except for sandy soils or soil covering heavy rainfall areas. Reduced leaf surface area, withering of the plant, and limited, highly branching root systems are some of the most common symptoms associated with chlorine deficiency. Near the leaf's tip, little patches of pale green chlorotic tissue emerge between the major veins. The old leaves show the first signs of chlorine deficit (**Figure 3**) [2]. The total chlorine content in the plant is very low. Chlorine accumulation in plants occurs in specific tissues, notably leaves or single cells (for example guard cells), causing toxicity.

In plants, chlorine-anion transporters have been found as homologous genes. They include ATP binding cassette (ABC) transporters, chloride intracellular channel (CLIC) and nucleotide sensitive–chloride conductance regulator protein (ICln) [93]. As proposed by a few researchers with studies on rice (7 members, OsCLC1-7) and Arabidopsis (7 members, AtClCa-g), members of the vast Chloride Channel (CLC) family were found in several organs [94]. They have been reported to encode anion channels/ion transporters that are essential in nitrate homeostasis [95]. Proteins from the CLC family of Arabidopsis were found in a variety of membranes, including the chloroplast membranes (AtClCd and AtClCf) (AtClCe), vacuolar membranes (AtClCa) and Golgi vesicles (AtClCd and AtClCf), and guard cells (AtClCc). AtClCa expression patterns in roots are very significant. They function as a $2\text{NO}_3^-/\text{K}^+$ exchanger, capable of accumulating nitrate in the vacuole using electrophysiological and genetic approaches in combination. The Cation-Cl-Cotransporters (CCC) proteins of *A. thaliana* (At CCC) catalyzed the coordinate symport of K^+ , Na^+ , and Cl^- in *Xenopus laevis* oocytes [96]. Recent advances in the identification of novel transporters of Cl^- have been reviewed by Li et. al., 2017 [67].

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