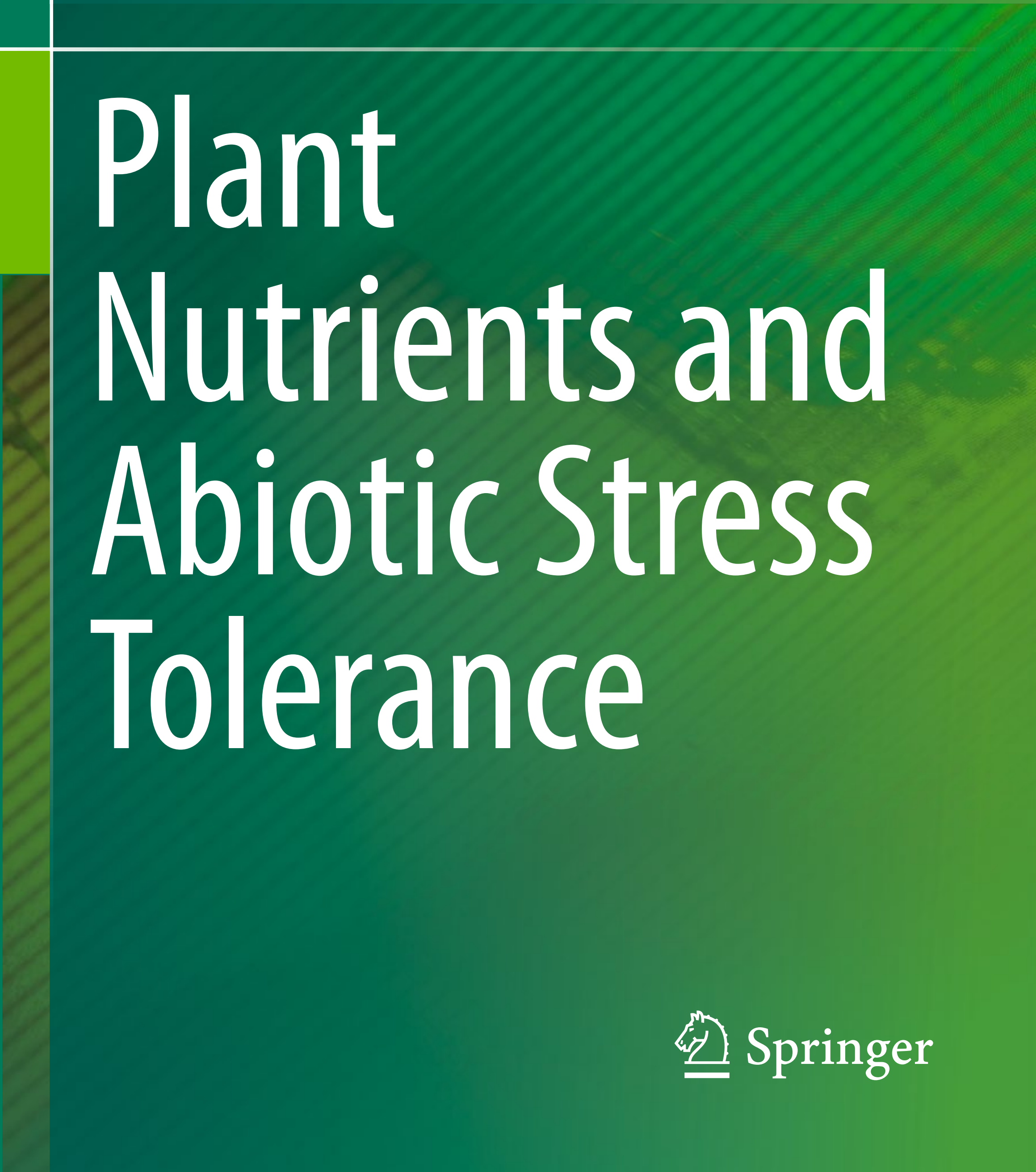
Mirza Hasanuzzaman · Masayuki Fujita
Hirosuke Oku · Kamrun Nahar
Barbara Hawrylak-Nowak *Editors*

Plant Nutrients and Abiotic Stress Tolerance



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Preface

Plant nutrients are the vital elements for plant growth and survival. Among the seventeen essential plant nutrients, only three (C, H and O) are derived from the atmosphere and the rest are supplied either from soil or by fertilizers. Each of the nutrients plays a unique role in plant life cycle and their requirement varies with the plant species and growth stages. Both the deficiency and excess of these nutrients render negative effects on plant growth and development. Besides, to ensure the efficient utilization of the nutrients, the environmental factors should be favourable.

Over the last few decades, abiotic stresses have turned into an important topic of concern for plant biologists. Numerous studies have been conducted and are still under experiment considering this fact that to survive the time-bound environmental changes, plants must possess some tolerance mechanisms within their cellular level. A large number of elements have been experimented among which plant nutrition has been a promising factor of study as it is an integral part of plant life cycle. Of all the plant nutrients, N, P, K, Mg, Mn, Cl and Fe are directly involved in plant photosynthetic activities; Ca, B, Cu, Fe, Mn, Zn and Mo are involved in enzymatic activities; N and S are involved in protein synthesis. These nutrients also play some more specific and crucial roles which are essential for sustaining normal plant biology and physiology. The unavoidable production of ROS during photosynthesis is intensified by the abiotic stress induced limited use of light energy and CO_2 fixation. Nutrients like N, K, Ca, Mg and Zn have been reported to maintain the utilization of light and CO_2 fixation and other photosynthetic activities to a required level. Especially K and Zn are observed to interfere with NADPH-oxidizing enzyme and as a result render protective roles against ROS-induced damages under abiotic stresses.

In the recent decades, some beneficial trace elements (such as Si and Se) at low concentration showed tremendous effect in conferring various abiotic stresses. Due to the advancement of science, intensive research works have been carried out globally to explore the underlying mechanisms of plant nutrient uptake, their metabolism, homeostasis and protection against abiotic stresses. Excellent review articles on the role of plant nutrients on abiotic stress tolerance have been published in journals, annual reviews and as chapters of some books. However, no comprehensive book on this topic has been published so far. Therefore, the objective of the book is to provide the insight into the latest findings on the role of plant nutrients in conferring abiotic stress tolerance to plants. This book will be a time-demanding topic for a large group of audience including plant scientists, agronomists, soil scientists, botanists, molecular biologists and environmental scientists.

We, the editors, would like to give special thanks to the authors for their outstanding and timely work in producing such fine chapters. We are highly thankful to Ms. Lee, Mei Hann, Editor (Editor, Life Science), Springer, Japan, for her prompt responses during the acquisition. We are also thankful to RaagaiPriya ChandraSekaran, Project Coordinator of this book and all other editorial staffs for precious help in formatting and incorporating editorial changes in the manuscripts. Special thanks to Dr. Md. Mahabub Alam, Noakhali Science and Technology University, Bangladesh, and Ms. Taufika Islam Anee, Sayed Mohammad Mohsin and Khursheda Parvin of Sher-e-Bangla Agricultural University, Bangladesh, for their generous help in formatting the manuscripts. The editors and contributing authors hope that this book will include a practical update on our knowledge for the role of plant nutrients in abiotic stress tolerance.

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Prof. Hasanuzzaman has published over 60 articles in peer-reviewed journals and books. He has edited 2 books and written 35 book chapters on important aspects of plant physiology, plant stress responses, and environmental problems in relation to plant species. These books were published by the internationally renowned publishers (Springer, Elsevier, CRC Press, Wiley, etc.). His publications got over 2000 citations with h-index: 23 (according to Scopus). Prof. Mirza Hasanuzzaman is a research supervisor of undergraduate and graduate students and supervised 20 MS students so far. He is Editor and Reviewer of more than 50 peer-reviewed international journals and recipient of "Publons Peer Review Award 2017." He is an active member of about 40 professional societies and acting as Publication Secretary of Bangladesh Society of Agronomy. He has been honored by different authorities due to his outstanding performance in different fields like research and education. He has received the World Academy of Science (TWAS) Young Scientist Award 2014. He has attended and presented 25 papers and posters in national and international conferences in different countries (USA, UK, Germany, Australia, Japan, Austria, Sweden, Russia, etc.).

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Barbara Hawrylak-Nowak is currently Associate Professor at the University of Life Sciences in Lublin, Poland. She earned her Master's degree in Biology (specialization: environmental biology) at the Department of Plant Physiology at Maria Curie-Skłodowska University in 2000. In the same year, she started doctoral studies at the Department of Plant Physiology, University of Life Sciences, Lublin. Barbara joined the team headed by Professor Maria Szymańska, which was focused on the biological activity of trace elements and mitigation of the effects of abiotic stress in crop plants. In 2002, she earned her Master's degree in Biotechnology at the Department of Molecular Biology, Maria Curie-Skłodowska University. She was granted the PhD degree in Agricultural Sciences in the field of Horticulture (specialization: plant physiology) in 2004. In her thesis, she pioneered investigations of the substrate pH-dependent biological activity of three chemical forms of selenium (selenite, selenate and selenomethionine) in three crop plant species. After completion of her Ph.D., Barbara accepted a position of Assistant Professor at the Department of Plant Physiology, University of Life Sciences in Lublin, where she worked for 13 years. During that time, she focused in particular on issues related to the application of trace elements and other phytoprotectants in mitigation of the impact of unfavourable environmental factors on plants, mineral nutrition of plants and ecological investigations. In 2017, Barbara was promoted to an Associate Professor position at the Department of Plant Physiology, University of Life Sciences in Lublin, where she has been working since that time. She also became the head of this department. Her teaching activity includes obligatory and facultative courses (lectures, laboratories) e.g. ‘Plant physiology’, ‘Non-infectious plant diseases’, ‘Plant under stress conditions’, ‘Biological adaptations of plants to the environment’, and ‘Physiology of woody plants’. As part of the didactic work, she conducts seminars and laboratories for graduate students performing engineering and Master’s research under her scientific supervision.

Barbara Hawrylak-Nowak has written over 40 refereed publications, including 25 papers published in journals indexed in JCR. Her research results were presented in over 35 conference reports at national and international scientific conferences. Her work has contributed to the knowledge of biological activity of trace elements in plants, especially grown under stressful conditions. She actively collaborates with several researchers/research groups in Poland and abroad.

Chapter 1
Biological Functions, Uptake and Transport of Essential Nutrients in Relation to Plant Growth

K. S. Karthika, I. Rashmi, and M. S. Parvathi

Abstract Plant nutrition takes care of the interrelationship between soil nutrients and plant growth. The role of nutrients in plant growth and physiology is dealt in this chapter in its maximum possible extent including the details on essential nutrients, their physiological roles, uptake and assimilation, nutritional disorders, the availability of nutrients in soil and their movement to plant roots and availability to plants by different modes of absorption. Every nutrient plays an indispensable role in carrying out physiological functions of plants enabling proper plant growth, the deficiency of which leads to particular disorders. Some nutrients are needed in larger quantities and some smaller but still essential for a plant to complete its life cycle. The primary roles of major nutrients in plant growth and physiology are widely studied and well documented. The functions of beneficial elements in plant nutrition may be investigated further. Soil, a complex substrate, acts as a storehouse of nutrients and water for plant growth. Plants have extensive root system for the nutrient uptake from the soil. However, the availability of all these nutrients in soil may fluctuate depending on so many factors. From the soil, nutrients move towards the roots by following certain mechanisms of transport, which include mass flow, diffusion and root interception. The nutrients thus reaching the roots are absorbed by plants either actively by spending energy or passively by no involvement of energy. Hence, a better understanding on plant nutrition would help to enhance crop productivity and nutritional value for the burgeoning world population.

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Keywords Mineral nutrients · Physiological functions · Plant growth · Deficiency · Toxicity · Growth laws

1.1 Introduction

For a healthy crop, adequate supply of nutrients is indispensable from soil. Thus healthy soils result in a healthy crop. Plant nutrition deals with the effect of nutrients present in the soil in plant growth and development. Plants form the basis of several food chains; hence, plant nutrition has impacts both on growth of plants and other living organisms (Maathuis 2009).

Every nutrient has a particular sufficiency range in plant. An imbalance in this range would affect the crop growth, and this imbalance could be either nutrient deficiency or toxicity. This could be a result of inadequate level of nutrient supply from the soil due to improper, inadequate and imbalanced application of fertilizers or nutrient sources. Toxicity occurs when a nutrient is above the sufficiency range than the plant needs, and this results in a decrease in growth of plant or its quality (McCauley et al. 2011). These disorders in plants are expressed as characteristic symptoms. As symptoms in plants arise due to several factors like pests, diseases, nutrient deficiency, toxicity, etc., it becomes important to identify the exact reason.

Deficiencies and toxicities of nutrients adversely affect crop health resulting in the appearance of unusual visual symptoms, thereby decreasing crop productivity. According to McCauley et al. (2011), the role and mobility of each essential nutrient need to be well understood as to determine which nutrient is responsible for a particular symptom, whether deficiency or toxicity. A proper focus on the knowledge on role of nutrients in plant growth is therefore important. Hence, a better understanding on plant nutrition would help to enhance crop productivity and nutritional value for the burgeoning world population. The role of nutrients in plant growth and physiology is dealt in this chapter in its maximum possible extent including the details on essential nutrients, their physiological roles, uptake and assimilation, nutritional disorders, the availability and status of nutrients in soil and their movement to plant roots and availability to plants by different modes of absorption.

1.2 Essential Nutrients

1.2.1 Criteria for Essentiality

An element is considered as essential when the three criteria as proposed by Arnon and Stout (1939) are met. These include:

1. A deficiency of the element makes it impossible for the plant to complete its life cycle.
2. The deficiency is specific to the element and can be prevented or corrected only by supplying the element in question.

Table 1.1 Critical information on nutrients in relation to plants

Nutrient	Essentiality discovered by	Year of discovery	Plant-usable form	Average conc.in plant tissue	Relative number of atoms compared to Mo as one
H	Since time immemorial		H_2O	6%	60,000,000
O	Since time immemorial		H_2O and O_2	45%	30,000,000
C	Priestley et al.	1800	CO_2	45%	30,000,000
N	Theodore de Saussure	1804	NO_3^-, NH_4^+	1.5%	1,000,000
K	C. Sprengel	1839	K^+	1.0%	400,000
Ca	C. Sprengel	1839	Ca^{2+}	0.5%	200,000
Mg	C. Sprengel	1839	Mg^{2+}	0.2%	100,000
P	C. Sprengel	1839	$H_2PO_4^-$, HPO_4^{2-}	0.2%	30,000
S	Sachs and Knop	1860	SO_4^{2-}	0.1%	30,000
Cl	T.C. Broyer, A.B. Carlton, C.M. Johnson and P.R. Stout	1954	Cl^-	100 mg kg^{-1}	3000
Fe	E. Gris	1843	Fe^{2+}	100 mg kg^{-1}	2000
B	K. Warington	1923	H_3BO_3, $H_2BO_3^-$, HBO_3^{2-}, BO_3^{3-}	20 mg kg^{-1}	2000
Mn	J.S. McHargue	1922	Mn^{2+}	20 mg kg^{-1}	2000
Zn	A.L. Sommer and C.P. Lipman	1926	Zn^{2+}	20 mg kg^{-1}	300
Cu	A.L. Sommer, C.P. Lipman and G.McKinney	1931	Cu^{2+}	6 mg kg^{-1}	100
Mo	D.I.Arnon and P.R. Stout	1939	MoO_4^{2-}	0.1 mg kg^{-1}	1
Ni	P.H.Brown, R.M. Welch and E.E.Cary	1987	Ni^{2+}	0.1 mg kg^{-1}	–

Source: Tisdale et al. (1997)

3. The element is directly involved in the nutrition of the plant, for example, as a constituent of an essential metabolite or needed for the action of a particular enzyme system.

Based on these criteria, the following elements are considered essential for higher plants. There are 17 essential nutrients recognized for growth of plants. These are carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulphur (S), iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), boron (B), molybdenum (Mo), chlorine (Cl) and nickel (Ni). Carbon (C), hydrogen (H) and oxygen (O) are obtained primarily from water and carbon dioxide; hence these are not considered mineral nutrients (Taiz and Zeiger 2002). Critical information on these essential nutrients is presented in Table 1.1.

1.3 Classification of Nutrients

1.3.1 Classification Based on Quantity

Essential nutrients are classified into macronutrients or micronutrients on the basis of their relative concentration in plant tissue. This is the quantity-based classification (Rattan 2015).

1.3.1.1 Major or Macronutrients

Those nutrients that are required by plants in large quantities are classified under major or macronutrients. These include C, H, O, N, P, K, Ca, Mg and S. Among these N, P and K are called primary nutrients and Ca, Mg and S form the secondary nutrients.

Primary Nutrients: Nitrogen (N), phosphorus (P) and potassium (K) are the primary nutrients as they are required in larger quantities by plants. Application of fertilizers containing N, P and K would help in correcting these deficiencies once noticed.

Secondary Nutrients: Calcium (Ca), magnesium (Mg) and sulphur (S) are secondary nutrients due to their moderate requirements by plants and localized deficiencies (Rattan 2015).

1.3.1.2 Micronutrients

Those nutrients that are required by plants in relatively lesser quantities but as essential as macronutrients are classified as micronutrients. These include Fe, Mn, Zn Cu, Ni, B, Mo and Cl. Micronutrients can be cationic (Fe, Mn, Zn, Cu, Ni) and anionic (B, Mo and Cl) in nature. Cationic micronutrients are absorbed as the divalent cations and anionic micronutrients are absorbed in anionic forms by the crops. Boron could also be taken up as neutral H_3BO_3 molecule by the plants.

There are certain elements that promote plant growth and essential for some but not for all higher plant species. These are classified as *beneficial elements*. These include silicon (Si), sodium (Na), cobalt (Co) and selenium (Se). These elements promote growth for different species under different environmental conditions. However, for each element and plant species, the roles played by these nutrients and their concentration vary (Pilon-Smits et al. 2009).

1.3.2 Classification Based on Biochemical Behaviour

A classification based on the biochemical properties is arrived at as the classification based on relative concentration in plant tissues does not take into consideration the physiology of higher plants and the role of nutrients in plant physiology on a

Table 1.2 Classification of plant nutrients based on biochemical behaviour

Nutrient	Biochemical functions
Group 1	Nutrients that are part of carbon compounds
N	Constituent of amino acids, amides, proteins, nucleic acids, nucleotides, coenzymes, hexoamines, etc.
S	Component of cysteine, cystine, methionine and proteins. Constituent of lipoic acid, coenzyme A, thiamine pyrophosphate, glutathione, biotin, adenosine-5′-phosphosulphate and 3-phosphoadenosine
Group 2	Nutrients that are important in energy storage or structural integrity
P	Component of sugar phosphates, nucleic acids, nucleotides, coenzymes, phospholipids, phytic acid, etc. Has a key role in reactions that involve ATP
Si	Deposited as amorphous silica in cell walls. Contributes to cell wall mechanical properties, including rigidity and elasticity
B	Complexes with mannitol, mannan, polymannuronic acid and other constituents of cell walls. Involved in cell elongation and nucleic acid metabolism
Group 3	Nutrients that remain in ionic form
K	Required as a cofactor for more than 40 enzymes. Principal cation in establishing cell turgor and maintaining cell electroneutrality
Ca	Constituent of the middle lamella of cell walls. Required as a cofactor by some enzymes involved in the hydrolysis of ATP and phospholipids. Acts as a second messenger in metabolic regulation
Mg	Required by many enzymes involved in phosphate transfer. Constituent of the chlorophyll molecule
Cl	Required for the photosynthetic reactions involved in O_2 evolution
Mn	Required for activity of some dehydrogenases, decarboxylases, kinases, oxidases and peroxidases. Involved with other cation-activated enzymes and photosynthetic O_2 evolution
Na	Involved with the regeneration of phosphoenolpyruvate in C4 and CAM plants. Substitutes for potassium in some functions
Group 4	Nutrients that are involved in redox reactions
Fe	Constituent of cytochromes and non-haem iron proteins involved in photosynthesis,N_2 fixation, and respiration
Zn	Constituent of alcohol dehydrogenase, glutamic dehydrogenase, carbonic anhydrase, etc.
Cu	Component of ascorbic acid oxidase, tyrosinase, monoamine oxidase, uricase, cytochrome oxidase, phenolase, laccase and plastocyanin
Ni	Constituent of urease. In N2-fixing bacteria, constituent of hydrogenases
Mo	Constituent of nitrogenase, nitrate reductase and xanthine dehydrogenase

Source: After Evans and Sorger (1966) and Mengel and Kirkby (1987)

large scale. Hence, this classification is adopted as proposed by Mengel and Kirkby (1987). The classification is presented in Table 1.2 in which nutrients are classified under four basic groups.

1. Firstly, those elements that are involved in the formation of organic compounds in the plant which are assimilated by the plants through biochemical reaction involving oxidation and reduction (redox reactions).

2. Secondly, elements that are present in the reactions with involvement of energy storage and for structure maintenance. Phosphorus, silicon and boron contribute to carry out these functions.
3. Those nutrients present in ionic forms are classified in this third group, such as those that serve the functions of cofactors and in osmoregulation.
4. Nutrients involved in redox reactions are classified in the fourth group.

1.4 Role of Nutrients in Plant Growth and Physiology

The role of nutrients in plant growth including their assimilation, physiological functions, nutrient deficiency symptoms and toxicity symptoms are described individually hereunder.

1.4.1 Nitrogen

Nitrogen is required by plants in greatest amounts. Nitrogen, being a very mobile element, circulates well between the atmosphere, the soil and the living organisms. Nitrogen-sufficient plants contain 1–5% of N (10,000–50,000 ppm or mg kg^{-1} dry matter).

1.4.1.1 Uptake and Assimilation

Nitrogen is absorbed either as nitrate (NO_3^-) ion, the prevalent form of uptake, or as ammonium (NH_4^+) ion depending on plant species and the conditions of soil like pH and redox state. Under reduced conditions, such as in the case of rice, N is taken up in ammoniacal form. Nitrogen, up on reduction, attains its −3 valence state for its assimilation and uptake. Nitrate reductase and nitrite reductase are the two important enzymes that ensure the conversion of nitrate (NO_3^-) to ammonium (NH_4^+). The translocation of nitrogen in higher plants takes place mainly as nitrate and amino acids mainly through the xylem from the roots towards the upper plant parts. High-affinity H^+-coupled symporters belonging to the NRT family mediate NO_3^- uptake. MT transporters or NH_3/H^+ symporters mediate NH_4^+ uptake. Nitrate reduction and assimilation occur mostly in the shoot. The mechanism of N uptake and assimilation is represented in Fig. 1.1.

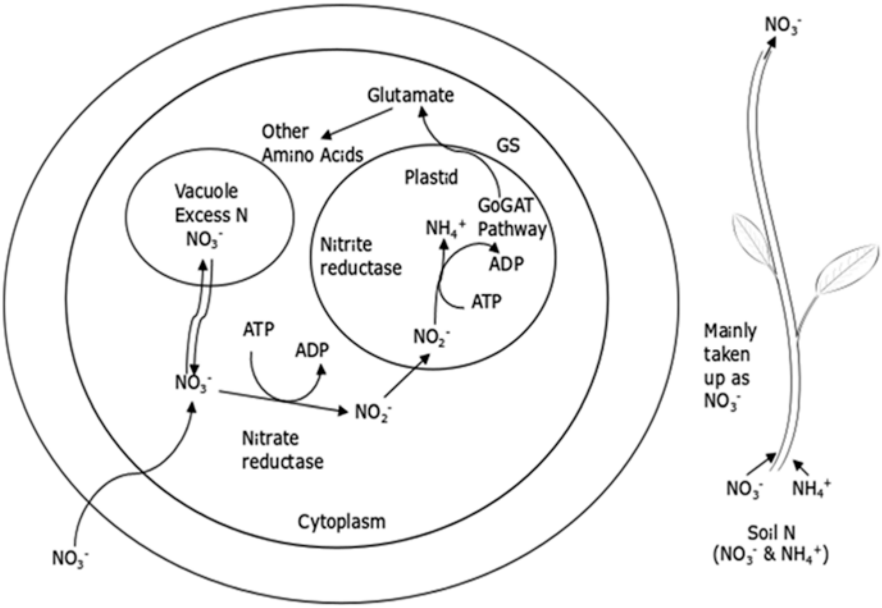

Fig. 1.1 Mechanism of N uptake and assimilation. Enzyme nitrate reductase reduces nitrates to nitrites in the cytoplasm. Reduction of nitrites to ammoniacal form occurs in chloroplasts with the help of enzyme nitrite reductase. Ammoniacal N is assimilated into the amino acid glutamate. The excess nitrogen is stored in vacuoles as nitrates

1.4.1.2 Physiological Functions

- Nitrogen is an important constituent of several plant cell components. It is an essential component of nucleic acids, proteins, amino acids, phospholipids and many other secondary metabolites. The amino groups in amino acids are provided by the element N, which thereby remains its foremost function.
- Nitrogen is present in the ring structure of purine and pyrimidine bases of nucleotides, which form the basis of nucleic acids. As the component of nucleic acid either as deoxyribonucleic acid (DNA) or as ribonucleic acid (RNA), N holds its responsibility in the transfer of genetic code to the offsprings (Rattan 2015)
- Chlorophyll, the pigment which imparts green colour to the leaves, contains N in it. Nitrogen due to its presence in chlorophyll enhances the quality of leaves, especially in leafy vegetables and fodders (Rattan 2015).
- The proportion of amino acids like glutamic acid ($C_5H_9NO_4$), proline ($C_5H_9NO_2$), phenylalanine ($C_9H_{11}NO_2$), cysteine ($C_6H_{12}N_2O_4S_2$), methionine ($C_5H_{11}NO_2S$) and tyrosin ($C_9H_{11}NO_3$) are enhanced, and the amounts of lysine ($C_6H_{14}N_2O_2$), histidine ($C_6H_9N_3O_2$), arginine ($C_6H_{14}N_4O_2$), aspartic acid ($C_4H_7NO_4$), threonine ($C_4H_9NO_3$), glycine ($C_2H_5NO_2$), valine ($C_5H_{11}NO_2$) and leucine ($C_6H_{13}NO_2$) in the grain are decreased with nitrogen fertilization. This improves quality of protein in the food grains (Rattan 2015).

- Nitrogen is found to play an essential role in the biochemistry of coenzymes, photosynthetic pigments which are nonprotein compounds. In ample supply, nitrates get deposited in the vacuole. This plays an important role in turgor generation (Maathuis 2009).

1.4.1.3 Deficiency Symptoms

- Nitrogen deficiency inhibits overall growth of the plant. The symptoms include yellowing or chlorosis of leaves due to a collapse in chloroplasts. Since N is mobile in plants, the deficiency appears in the older leaves near the base of the plant. Later it advances towards the younger leaves under conditions of severe deficiency. This may lead to necrosis of entire leaf or parts of the leaf (Agarwala and Sharma 1976).
- The plants appear small with spindly stems. Nitrogen deficiency results in smaller leaves, and there occurs premature falling of older leaves. Branching of roots gets restricted and this adversely affects the root growth. However an increase in the root/shoot ratio is observed with nitrogen deficiency (Mengel and Kirkby 2006).
- Amino acids especially Gln, proteins and chlorophyll content are found to decrease with a deficiency in N. Nitrogen starvation could also lead to an increase in starch and specific flavonoids (e.g. rutin and ferulic acid) and phenyl propanoids (Amtmann and Armengaud 2009).
- In cereals nitrogen deficiency results in decreased tillering, reduction in the number of ears per unit area and also the number of grains per ear. Though the grains remain small, protein concentration remains relatively higher. This is attributed to the decrease in the import of carbohydrate into the grains which takes place at the later stages of grain filling (Mengel and Kirkby 2006). Nitrogen deficiency characterized by pale green or yellowish leaves of corn is shown in Fig. 1.2.
- In case of nitrogen deficiency, synthesis of anthocyanin results due to the nonusage of carbohydrates in nitrogen metabolism, leading to its accumulation. In tomato and certain varieties of corn, nitrogen deficiency is observed as purple coloured leaves, stems and petioles (Taiz and Zeiger 2002).
- In cocoa, leaves turn pale yellow in colour and are reduced in size in case of nitrogen deficiency. Older leaves exhibit scorching at the tip, and petioles make an acute angle with the stem.

1.4.1.4 Toxicity Symptoms

Excess of nitrogen contributes to darker green colouration of leaves and succulent growth of plants. The plants grow taller with heavier heads succumbing plants to easy lodging. Thick succulent growth attracts insect, pest and disease attacks (Rattan 2015).

Fig. 1.2 N deficiency in corn. (Photo: by K.S. Karthika)

1.4.2 Phosphorus

Phosphorus is the second most abundant mineral in the human body. In the soil, the dominant form in which phosphorus occurs is orthophosphate ion, whereas in plants, it also occurs in pyrophosphate form to a minor extent. Phosphorus is considered to be an immobile element in soils and mobile element in plants. The P concentration in plants with sufficient P varies from 0.1 to 0.4% by weight, which is 1/5 to 1/10 of N or K content (Rattan 2015).

1.4.2.1 Uptake and Assimilation

Phosphate taken up directly as inorganic PO_4^{3-} (Pi) by roots is xylem translocated. It moves to the fast-growing young laminae in its oxidized form. Inorganic P forms occur mainly as soluble Pi (orthophosphate) or as PP (pyrophosphate). Newer leaves receive phosphate both from the roots and from the older leaves. This was observed in a study to understand the transport and assimilation of P on castor bean by Jeschke et al. (1997). Organic P upon hydrolysis is translocated via the phloem. The mechanism of P uptake and assimilation is represented in Fig. 1.3.

1.4.2.2 Physiological Functions

- Phosphorus is an important constituent in the structure of nucleic acids and lipid membranes.

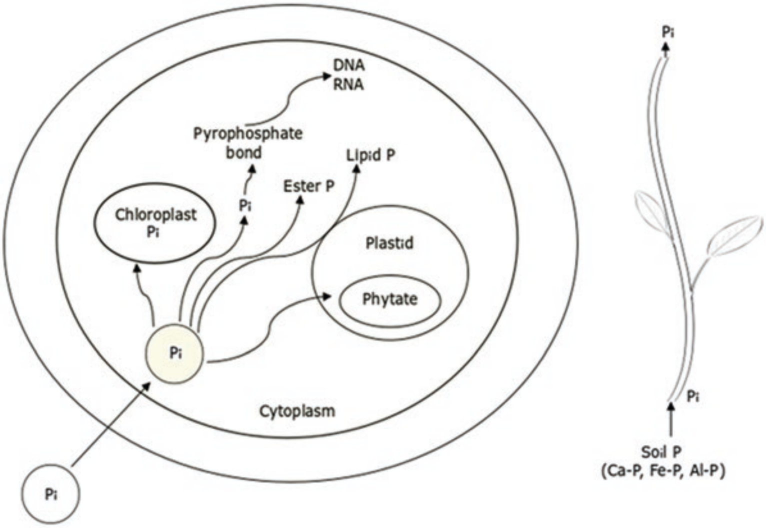

Fig. 1.3 Mechanism of P uptake and assimilation. H^+-coupled high-affinity transporters mediate the direct uptake of P in the form of inorganic PO_4^{3-} (Pi). Inorganic P (Pi) inside the cells forms high-energy pyrophosphate and ester bonds. This Pi is an essential component of lipid membrane in maintaining the integrity of membrane. In chloroplasts, Pi is essential during photosynthesis in the formation of high-energy bonds. Pi enters the chloroplast in exchange for glyceraldehyde-3-phosphate (G3P). Phosphorus is stored as phytate together with minerals in plastids

- Phosphorus is an important component of adenosine triphosphate (ATP). Phosphorus is involved in all energy transfer reactions in the cell, as ATP is known as the energy currency of the cell.
- Phosphorus is involved in photosynthesis, translocation of sugars and starch, movement of nutrients within the plant and transfer of genetic characteristics from one generation to the next as it is a component in DNA and RNA (Taiz and Zeiger 2002).
- It plays an indispensable role in the formation of flower and seeds and in the growth of plant. Root proliferation is enhanced by P, and thus it helps the plant to explore bigger soil volume for water and nutrients. Phosphorus has another essential role in cellular metabolism. Large amounts of P are stored in seeds to enable embryo development, germination and seedling growth (Marschner 1995).
- Rhizobium bacteria which convert atmospheric nitrogen (N_2) into ammoniacal (NH_4^+) form have P as an essential ingredient. Nodule development in nitrogen-fixing legumes is enhanced by the availability of P as it is an energy source.
- It reduces the severity of crop diseases and increases resistance to drought and salinity. Phosphorus enhances water use efficiency of crops under limited soil moisture conditions.

- Phosphorus also influences several quality factors, and these include lower moisture and higher sugar content of grains, reduced losses due to diseases, improvement in marketable yield fraction and enhanced feed value (Rattan 2015).

1.4.2.3 Deficiency Symptoms

- Phosphorus is considered to be deficient in plants when the concentration falls below 0.1% or 1000 ppm P (Rattan 2015).
- Phosphorus deficiency affects the overall growth of plant. Since phosphorus is a mobile element in plants, its deficiency symptoms appear initially on the older leaves.
- Excess anthocyanin synthesis is observed with P deficiency giving the leaves a slight purple colouration. Phosphorus deficiency purple colour is not due to the chlorosis in contrast to nitrogen deficiency. Thus particular P deficiency symptoms are observed as dark greenish purple leaves which get malformed. There will be necrotic spots on the leaves. The overall growth of young plants gets stunted (Taiz and Zeiger 2002).
- When P is deficient, stems of many annual plant species may appear reddish due to an enhanced formation of anthocyanin. Leaf expansion gets inhibited with a reduction in leaf surface area as one of the symptoms in the case of P deficiency (Fredeen et al. 1989).
- Phosphorus deficiency results in reduced tillering in cereals, reduced rates of new shoots and flower formation in fruit trees, premature drying and shedding of leaves, poor growth and shortening of fronds in coconut palms.
- In coconut, as an initial symptom, leaves become purple coloured, and in severe cases, leaves may turn yellow. Premature drying and shedding of leaves are also seen. Fronds become shortened and growth gets restricted in case of P deficiency.

1.4.3 Potassium

Potassium is taken up by plant roots in its cationic form, i.e. K^+. The main natural source of K^+ is the weathering of K-bearing minerals. Potassium exists in a dynamic equilibrium in soil and it is highly mobile in plants. Potassium concentration in healthy plant tissues varies from 1% to 5%. Though potassium does a regulatory role in plant metabolism and development, it does not form a structural component of the plant (Rattan 2015).

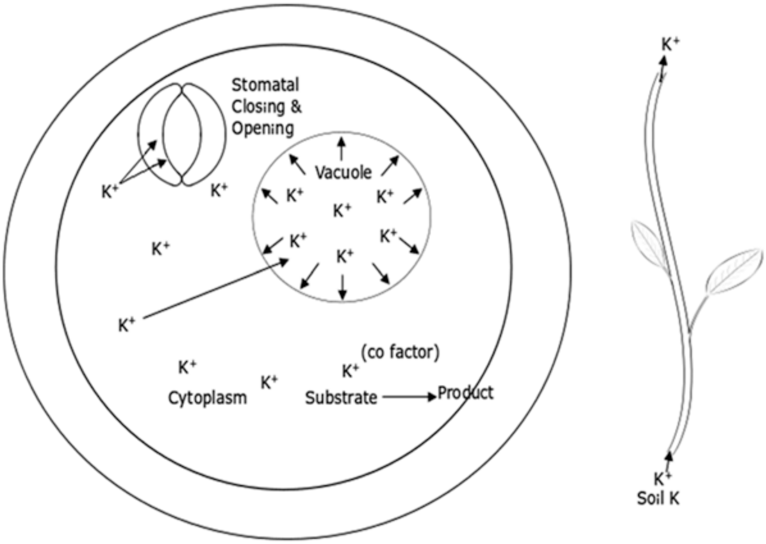

Fig. 1.4 Mechanism of K uptake and assimilation. H^+-coupled high-affinity symporters mediate potassium uptake. Potassium is also taken up through low-affinity ion channels. Potassium acts as a cofactor in enzymatic reactions between substrates and products. It generates turgor to provide structure and drive cell expansion as the main cation in vacuoles. Potassium is also involved in the regulation of stomatal apertures

1.4.3.1 Uptake and Assimilation

Potassium is taken up and translocated throughout the plant at high rate and efficient means. Various K^+ uptake systems become the reason for the higher rate of uptake of potassium which is facilitated by specific channels in the plasmalemma and tonoplast of plant tissues. Potassium is highly mobile in plants, and K translocation takes place via both xylem and phloem. In xylem, root to shoot transport of K^+ takes place. Whereas via phloem, transport of K^+ is towards sink organs. This may be seeds or fruits in the shoot or tubers and the storage roots (beets). The mechanism of K uptake and assimilation is represented in Fig. 1.4.

1.4.3.2 Physiological Functions

- The foremost role of potassium is in enzyme activation. It helps in more than 60 enzymes, and it includes many enzymes involved in respiration and photosynthesis (Rattan 2015). Potassium involves directly in the activation of enzymes like pyruvate kinase and starch synthase.
- Since potassium is important in ATP production and is involved in regulating the photosynthesis rate, with its deficiency, photosynthesis and ATP production rates

are reduced. This results in slowing down of all the ATP-dependent processes (Rattan 2015).
- Potassium helps in improving the efficiency of photosynthesis and CO_2 assimilation. In photosynthesis, at the site of ATP production, K maintains electrical charge balance (Uchida 2000).
- The functions of K in photosynthesis and ATP production relegate its stomatal activity-related function to the second position. It helps in maintaining the water balance of plants by controlling the turgor involved in the stomatal opening and closure process. It helps in regulating the osmotic pressure in plant cells (Maathuis 2009).
- Nutrients and water transport via xylem and photosynthate transport via phloem are improved with potassium (Mengel and Kirkby 2006).
- Known as the quality element/nutrient, potassium is very important in maintaining crop quality. It is significant in improving disease resistance, drought tolerance and shelf life of fruits and vegetables.

1.4.3.3 Deficiency Symptoms

Symptoms of potassium deficiency are observed initially on older leaves as the element is highly mobile in plants. Protein synthesis is adversely affected and seldom synthesised with the deficiency of potassium even with the availability of nitrogen. Instead, precursors for the synthesis of proteins such as amino acids, amides and nitrate accumulate. Visual symptoms are immediately not resulted in the case of potassium deficiency; however initial symptoms include a fall in the rate of plant growth (Hidden hunger) (Dawson 2014).

- The visual symptoms appear as chlorosis of older leaves. This begins at the leaf margins, which later progresses inwards. Leaves curl and crinkle towards advanced stages of deficiency.
- Potassium deficiency affects the lignification of the vascular bundles, which in turn leads to lodging of crops.
- The stems of potassium-deficient plants may have shorter internodes and also occur slender and weak (Taiz and Zeiger 2002).
- In coconut palms, deficiency of K causes orangish yellow discolouration from the tip of the leaflets, progressing along the margin towards the base. In case of severe deficiency, tip of leaflets withers and becomes necrotic. The midrib remains green, and some leaves exhibit a scorched appearance (Fig. 1.5). In general, growth of the K-deficient coconut palm gets reduced, with slender trunk, shorter leaflets and reduced number of inflorescences, nut set and nuts per bunch.
- Potassium deficiency symptoms in areca palm begin on leaves as necrotic speckling. This gives a light brown-coloured appearance to the leaf. Leaf margin and tip scorching are commonly observed in case of K deficiency. Canopy size and trunk diameter get reduced in advanced stages of K deficiency.

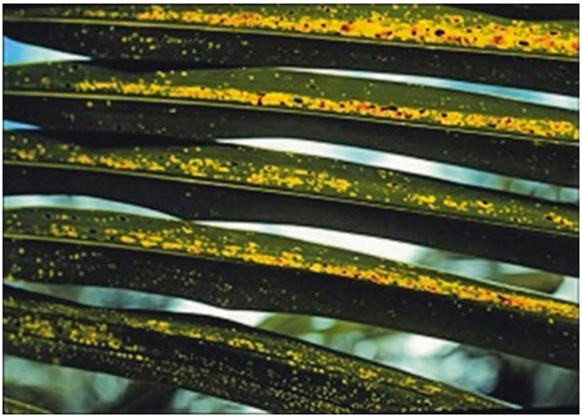

Fig. 1.5 K deficiency symptoms in coconut leaf. (Photo: T.K.Broschat)

- In cocoa, potassium deficiency is characterized by necrosis which begins as yellowish areas in the interveinal regions along the margins. This marginal necrosis later progresses between veins as the deficiency of K advances (Wood and Lass 1985).
- Deficiency of K in soils may affect the stem, lead to lodging of corn plants, and also increase the susceptibility of corn roots to root-rotting fungi (Taiz and Zeiger 2002).

1.4.3.4 Toxicity Symptoms

Potassium can be accumulated in abundant amounts without exhibiting toxicity symptoms within the plants, and this behaviour is described as the *luxury consumption* of potassium.

1.4.4 Calcium

Calcium is very abundant in lithosphere similar to potassium. Uptake of calcium by plants is mainly in the form of Ca^{2+}. Calcium is mobile in soil and relatively immobile in plants. In plants Ca content ranges between 0.2% and 1.0% (Rattan 2015).

1.4.4.1 Uptake and Assimilation

Calcium (Ca^{2+}) permeable channels which could be Ca^{2+} selective or Ca^{2+} non-selective ion channels allow the entry of calcium towards the root. Calcium ion (Ca^{2+}) remains sequestered in the vacuole of mature cells, with calcium being immobile in plants. This process occurs with the involvement of members of the CAX H^+/Ca^{2+} antiport family and by ATP-driven P-type ATPases (McAinsh and Pittman 2009).

1.4.4.2 Physiological Functions

- Calcium is essential in plant growth and development. It plays an important role in meristematic growth. Dominant functions of Ca^{2+} which are cellular are mainly structural.
- Calcium is better known as a secondary messenger as it is required for the normal functioning of plant membranes. In several cases of responses of plants to hormonal and environmental signals, it functions well as a second messenger (Sanders et al. 1999). Calmodulin is a protein found in the cytosol of plant cells. When Ca functions as a second messenger, it binds to calmodulin and forms calmodulin-calcium complex, which thus plays an essential role in regulating many metabolic processes
- Calcium pectate is the major constituent of cell wall providing rigidity to it. Thus it helps in maintaining the integrity of cell membrane.
- Calcium plays a role in cell elongation and cell division (mitosis), and it also helps to maintain the structure of chromosomes.
- In the case of imbalances in nutrient ions in soil, soil reaction, Al^{3+} toxicity, etc., root cells are protected by calcium.
- Nitrogen assimilation into organic constituents, especially proteins, is favoured by calcium. High supply of Ca may be a prerequisite for making symbiotic leguminous plants susceptible to infection by *Rhizobium* (Rattan 2015).
- Calcium is involved in the activation of enzymes like phospholipase, arginine kinase, amylase and ATPase.

1.4.4.3 Deficiency Symptoms

The deficiency of Ca occurs seldom relatively as most of the soils are abundant in soil available calcium. But in cases of severe weathering and extreme leaching of soils, deficiency of Ca may occur. This condition is accelerated by lowering of pH in the soils. Calcium being immobile in plants, the deficiency symptoms may begin to appear in the younger leaves. When the concentration of Ca in plants falls below 0.1% (or 1000 ppm), it is considered as Ca deficient (Rattan 2015).

- Meristematic tissues are affected negatively in the case of calcium deficiency. Characteristic symptoms of Ca deficiency include younger leaves appearing small, deformed and chlorotic. As the deficiency advances, the leaves turn necrotic. The leaves turn cup shaped and crinkled, and the terminal buds deteriorate with breaking down of petioles. The stem gets weakened, and root system appears brownish, short, branched and stunted on Ca deficiency (Mengel and Kirkby 2006).
- The common Ca deficiency symptoms include:

  1. Blossom end rot in tomatoes (Fig. 1.6)
  2. Bitter pit in apples
  3. Black heart in celery

Fig. 1.6 Ca deficiency in tomato – blossom end rot. (Photo: Scot Nelson, University of Hawaii)

4. Internal browning in Brussels sprouts
5. Blossom end rot in pepper
6. Cavity spot in carrots

1.4.5 Magnesium

Magnesium is taken up by plants as Mg^{2+}. In soil and plants, magnesium is mobile in nature. Mg concentration in plants ranges between 0.1% and 0.4%. Concentration of Mg in soils varies between 0.05% and 0.5% (Maathuis 2009).

1.4.5.1 Uptake and Assimilation

The uptake of Mg^{2+} from soil solution is lesser than that of K^+, though Mg^{2+} concentration is relatively higher in soil. The translocation of Mg^{2+} towards storage tissues and fruits is promoted by potassium. Researchers have found that Mg^{2+} can be translocated from older to younger leaves or to the apex as it is very mobile in the phloem unlike Ca^{2+}. The transporters of MGT family favour the uptake of Mg^{2+} at the soil: root boundary. This action is similar to that of bacterial CorA Mg^{2+} transporters (Maathuis 2009).

1.4.5.2 Physiological Functions

- Magnesium occurs as a structural component in the central position of chlorophyll molecules and helps in imparting green colour to the leaves.

- Magnesium is involved in photosynthesis as light reactions in the stroma get promoted by the activity of Mg^{2+}. The key reaction of Mg^{2+} in photosynthesis is the activation of ribulose biphosphate carboxylase (Rubisco). Thus Mg provides a favourable effect on CO_2 assimilation and sugar and starch production (Maathuis 2009).
- Cellular Mg^{2+} serves a role as enzyme cofactor. Nucleotides and nucleic acids are stabilized with the help of Mg^{2+}. The best example is the role of Mg^{2+} in phosporylation/dephosphorylation and energy transfer. ATP, the energy source of the cell, becomes biologically active only when it is bound to magnesium ion. Phosphotransferases and ATPases release energy in the presence of Mg^{2+}. This is accomplished by the formation of a bridge at the protein catalytic site by the Mg^{2+} with the nitrogen atom present there and oxygen atoms on the phosphate group.
- Magnesium is an essential component of polyribosomes and the levels of Mg^{2+} determine the gene transcription and translation.
- Magnesium also helps in promoting the uptake of phosphorus and its translocation within the plants. Sugar transport within the plants also is improved by magnesium.

1.4.5.3 Deficiency Symptoms

Magnesium is adsorbed weakly on to the soil particles due to its small hydration shell. This leads to higher rates of Mg leaching from the soil and thereby Mg^{2+} deficiency. Lower amounts of Mg lead to a decrease in photosynthetic and enzyme activity within the plants. There occurs depolymerization of ribosomes on Mg deficiency resulting in premature ageing of the plants. The deficiency occurs when the concentration in plants falls below 0.1% Mg.

- Magnesium deficiency symptoms begin to appear in the older or lower leaves initially as the nutrient is mobile in plants. In the later stages, it moves to the younger leaves. The symptoms include interveinal chlorosis and streaked or patchy effects on leaves. Sometimes, the intercostal areas turn necrotic. In more advanced stages, the affected leaves turn smaller and curve upwards at margin. This may eventually result in drying of the tissues and death (Mengel and Kirkby 2006).
- The symptoms are similar in the case of cereals like wheat, maize, oats and rye during the initial stages, with an exception of maize taking on a more spotted appearance at later stages.
- "Grass tetany" is a particular example of Mg deficiency-related nutritional disorder common in cattles grazing on Mg-deficient pastures.
- In coconut palms, older leaves of palms exhibit Mg deficiency symptoms initially. Along the margins the leaves exhibit orange or bright lemon yellow colour whereas the leaf centre remains green in case of Mg deficiency (Fig. 1.7).

Fig. 1.7 Mg deficiency in coconut. (Photo: by Scot Nelson, University of Hawaii)

- In areca palms, the older leaves exhibit interveinal chlorosis leaving the midrib and veins green in colour. The chlorosis starts at the leaf tip progressing downwards and inwards along the margins and between the veins. Leaf margins curve upwards in the later stages.
- In cocoa, leaf necrosis of older leaves is the characteristic Mg deficiency symptom. This commences as necrosis near leaf margins in interveinal areas of leaves, later developing into marginal necrosis. The deficiency-free areas in leaves appear paler green. This develops a characteristic oak leaf pattern.

1.4.6 Sulphur

The most important S source for plants is SO_4^{2-}, a form which is mobile in soils. Sulphur concentration in plants varies between 0.1% and 0.4%, similar to that of P and Mg. Sulphur is very important in oilseed crops as these crops require more S than cereal grains. For example, the amount of S required to produce 1 ton of seed is about 3–4 kg for cereals (range 1–6), 8 kg for legume crops (range 5–13) and 12 kg for oil crops (range 5–20) (Jamal et al. 2010).

1.4.6.1 Uptake and Assimilation

Sulphur is taken up mainly in the form of sulphates and it is highly mobile in plants. The uptake and movement of sulphates are facilitated by H^+ gradient energized sulphate transporters. Transport of S takes place as sulphate ions via xylem to the shoot, and it undergoes reduction. The sulphate ions get reduced mainly in shoot chloroplasts and some in root plastids. Thus the reduction of SO_4^{2-} to SO_3^{2-} and to S^{2-} is essential for the assimilation of sulphur. The amino acid cysteine contains S^{2-} the highly reduced form. Sulphur that is present in excess gets accumulated as SO_4^{2-} in vacuoles (Maathuis 2009).

1.4.6.2 Physiological Functions

- Amino acids like cysteine ($C_3H_7NO_2S$), cystine ($C_6H_{12}N_2O_4S_2$) and methionine ($C_5H_{11}NO_2S$-$HO_2CCH(NH_2)CH_2CH_2SCH_2$) contain sulphur as an essential constituent. It is also present in several coenzymes and vitamins essential for metabolism. For example, CoA and vitamins like biotin and thiamine have sulphur as its constituent.
- In onions, volatile sulphur compounds (disulphides or polysulphides) are present which attributes to the effect of bringing tears to the eyes, i.e. lachrymatory effect. Diallyl disulphide is the main component in garlic oil. In mustard oil, various glucosides are synthesised which is favoured by S. Thus S helps in improving the oil quality in oilseed crops.

1.4.6.3 Deficiency Symptoms

Sulphate ion is relatively weakly bound to soil than phosphate ions. Thus it gets easily leached off in cases of heavy rainfall. This results in the depletion of sulphur from soils. Sulphur, being a constituent of proteins, its synthesis is inhibited with the deficiency of S. Deficiency of S occurs when the concentration in plants is less than 0.1–0.2%. Sulphur deficiency symptoms are mainly characterized by chlorosis. This results in stunted growth and accumulation of anthocyanin. These are similar to nitrogen deficiency symptoms (Taiz and Zeiger 2002).

- Sulphur deficiency occurs in younger leaves first. Sulphur being immobile in plants, deficiency symptom is initially observed in mature and young leaves. The symptoms arise as interveinal chlorosis. Sulphur deficiency chlorosis can occur in all leaves at the same time or only in the older leaves initially in many plant species (Taiz and Zeiger 2002).
- Typical symptoms of S deficiency include yellowish-green or yellowish-orange leaflets in the case of coconut palm. With the weakening of stem, drooping of leaves is observed as sulphur deficiency symptom. Decrease in the leaf number and a reduction in size of leaves are seen in older palms. The number of live fronds becomes fewer. In the advanced stage, the crown loses most of the leaves, and severe necrosis is found on the older leaves (Southern 1969).
- In cocoa, leaves develop pale yellowish or yellowish green colouration. The size of leaves is not affected. Older leaves exhibit yellow blotches.

1.4.6.4 Toxicity Symptoms

Sulphur toxicity chances are seen in saline soils with excess concentration of sulphate salts; otherwise S toxicity seldom occurs. Sulphur toxicity could be in the form of atmospheric sulphate. This level may even raise up to 100 μg m^{-3} as a result of industries and burning of coal. According to Maathuis 2009 when the levels of S exceed 50 μg m^{-3}, the toxic effects could prove fatal to forest tree species. Higher levels of SO_2 in the atmosphere in few industrial regions have eradicated few lichen species. The toxicity symptom is seen as leaf necrosis.

1.4.7 Iron

Iron is taken up as ferrous ions (Fe^{2+}) by plants. Iron content ranges between 100 and 500 mg kg^{-1} of dry matter in plants. It exists in two oxidation states $Fe^{2+}$and Fe^{3+}in plants (Rattan 2015).

1.4.7.1 Uptake and Assimilation

Iron is taken up as Fe^{2+} through a specific channel of the plasma membrane. This is closely linked to the Fe^{3+} reduction. Either by diffusion or by mass flow, the iron (Fe^{3+}) siderophores in the soil are transported to the roots, and these enter the free space in the roots. Through these root-free spaces, these later move to the plasmalemma-bound Fe^{3+} reductase (Mengel and Kirkby 2006).

1.4.7.2 Physiological Functions

- Iron, a redox active metal is involved in several processes like mitochondrial respiration; photosynthesis; assimilation of nitrogen; biosynthesis of hormones like jasmonic acid, gibberellic acid and ethylene; osmoprotection; and production and scavenging of reactive oxygen species and pathogen defence (Hansch and Mendel 2009).
- Iron, present in cytochromes, plays a role in electron transfer in redox reactions. During electron transfer reactions, iron is reversibly oxidized from Fe^{2+} to Fe^{3+} (Taiz and Zeiger 2002).
- Three groups of iron-containing proteins, viz.:
    - (i) Fe-S proteins – These Fe-S proteins mainly play the roles as enzymes. For example, ferredoxin acts as electron carriers in electron transfer reactions. Another example is aconitase which functions as regulator protein (Hansch and Mendel 2009).
    - (ii) Haem-containing proteins – These contain Fe-porphyrin complex as a prosthetic group. The major haem proteins known are the respiratory and photosynthetic cytochromes enabling electron transfer (Hansch and Mendel 2009).
- Other iron proteins – These bind iron ions directly, also known as the non-haem proteins. Most prominent example includes the ferritins, which occur mostly in

etioplasts and amyloplasts (nongreen plastids) but not in green plastids which are the mature chloroplasts.
- Iron is involved in the metabolism of nucleic acids. Chlorophyll synthesis and its maintenance in plants demand the involvement of iron. (Rattan 2015).

1.4.7.3 Deficiency Symptoms

Occurrence of iron deficiency is relatively more on calcareous or saline alkali soils. When the concentration of iron in plants is less than 50 mg kg^{-1}, those plants are considered as iron deficient. The symptoms of iron deficiency appear initially on the younger leaves as Fe is immobile in plants. This distinguishes it from Mg deficiency (Taiz and Zeiger 2002).

- Iron deficiency is characterized by interveinal chlorosis. This begins to appear initially on the younger leaves. The margins and veins of leaves remain green. These veins later become chlorotic, under conditions of prolonged deficiency resulting in turning the entire leaf white. Growth gets affected severely turning the whole plant necrotic.
- In coconut, uniform chlorosis is the symptom associated with Fe deficiency. All the leaves from the top of the crown to the base will appear pale green or dark yellow in colour. There will be gradual yellowing of the leaflets in longitudinal strips parallel to the veins. In the advanced stages, the leaf becomes completely yellow. There will be shortening of the rachis and the leaflets. Under severe cases of Fe deficiency, newly formed leaflets develop necrotic tips. The palms will have a stunted growth eventually leading to the death of meristem (Broschat 2014a).

1.4.7.4 Toxicity Symptoms

- Iron (Fe) toxicity enhances the activity of enzyme polyphenol oxidase, as a result of oxidized polyphenols production. This thus causes leaf bronzing, the characteristic symptom of iron toxicity. Root oxidation power is negatively affected with the iron toxicity (Dobermann and Fairhurst 2000).
- Characteristic iron toxicity symptoms in rice include occurrence of small brown coloured spots on older/lower leaves beginning from tip. In advanced conditions, these spread towards the leaf base and combine on leaf interveins. This in turn results the whole leaf to turn orange yellow to brown in colour and die eventually. In case of severe Fe toxicity, leaves turn purple-brown. Tillering becomes limited resulting in stunted growth. This also affects the root system. Coarse, sparse, damaged roots are observed with dark brown to black coating on the surface of root as a result of Fe toxicity. Freshly uprooted rice hills tend to show poor root systems with many black and died roots (Dobermann and Fairhurst 2000).

1.4.8 Manganese

Manganese is taken up by plants in its cationic form of Mn^{2+}. Concentration of Mn in plants ranges between 20 and 300 mg kg^{-1} of dry matter. It can be easily oxidized into two oxidation states Mn^{3+} and Mn^{4+} in plants. Manganese resembles magnesium in its biochemical functions (Rattan 2015).

1.4.8.1 Uptake and Assimilation

Manganese is mainly taken up in the form of Mn^{2+}, and the uptake rates are lower than that of Ca^{2+} and Mg^{2+}. The uptake is mainly across the plasmalemma by facilitated diffusion. The translocation of Mn^{2+} ions via phloem is limited as the element is comparatively less mobile in plants. Manganese is preferentially translocated to meristematic tissues (Mengel and Kirkby 2006).

1.4.8.2 Physiological Functions

- Relevance of Mn in plant growth and metabolism is very high as manganese exists in many plant cell enzymes in three oxidation states: II, III and IV. This involves group of enzymes like oxidoreductases, hydrolases, lyases and ligases. (Hebbern et al. 2009).
- Manganese can fulfil two functions in proteins.
    (i) It serves as catalytically active metal: Mn-SOD (Mn-containing superoxide dismutase) helps in preventing damage of the cell from free radicals, the oxalate oxidase and the Mn-containing water-splitting system of photosystem II.
    (ii) It exerts an activating role on enzymes: Mn-activated enzymes include phenyl alanine ammonia lyase, isocitrate dehydrogenase, malic enzyme and PEP carboxykinase (Hansch and Mendel 2009).
- Manganese plays a unique role in water-splitting and oxygen evolution system in photosynthesis. The reaction involved is $2H_2O + 4e^- \rightarrow 4H^+ + O_2$. Manganese is linked with nitrogen assimilation in the plants due to its presence in nitrite reductase and hydroxylamine reductase enzymes.

1.4.8.3 Deficiency Symptoms

Deficiency occurs when concentration of Mn becomes less than 25 mg kg^{-1} dry matter. The deficiency resembles that of Mg deficiency; however the Mn deficiency symptoms initially appear on the younger leaves.

Fig. 1.8 Mn deficiency in coconut. (Photo: T.K. Broschat)

- In monocots, especially in oats, the symptom is termed as "grey speck". In this case, symptoms develop as grey spots or stripes at the basal region of the leaves. There will be a decrease in the turgor of the plants deficient in Mn. In later stages leaves wither as the upper part of the leaves breaks over near the middle (Mengel and Kirkby 2006).
- Interveinal chlorosis is the major symptom in dicots. Interveinal chlorosis in plants like apple, raspberry, cherry, peas, onion and French beans produce a "chequered effect" due to the appearance of yellowish leaf with the smallest leaf veins remaining green in colour (Rattan 2015).
- The common Mn deficiency symptoms are listed below.

  (i) Grey speck of oats
  (ii) Marsh spot of peas
  (iii) Speckled yellow of sugar beet
  (iv) Frenching of tung trees
  (v) Pahala blight of sugarcane

- In manganese (Mn)-deficient coconut palms, symptoms begin to appear on newer leaves. The symptoms begin as chlorosis of leaves, which later turns necrotic leading to withering of leaves. During withering the leaflets get curled about the rachis. The characteristic symptom in coconut leaf is termed as "frizzle top" as the withering gives a frizzled appearance to the leaf. The growth gets stunted in case of severe Mn deficiency, and the emerging leaves will be with petiole stubs affected with necrosis (Fig. 1.8; Broschat 2014b).
- Manganese deficiency symptoms in cocoa develop as blurred chlorosis in younger leaves. The leaves appear pale yellow or yellowish green in colour with the veins remaining green. The tip and distal margins get scorching in case of severe deficiency.

1.4.8.4 Toxicity Symptoms

Manganese toxicity occurs with higher concentrations of Mn^{2+} which happens under highly reduced conditions like in flooded conditions. Acid to very acid soils also contain toxic concentrations of manganese. This toxicity is seen especially in acid sulphate soils where the soil pH falls below 3.0. Toxicity symptoms develop in the older leaves as brown spots of MnO_2 enclosed by chlorotic areas.

In cocoa, Mn toxicity symptoms appear on leaves as yellowish or pale green areas that are irregular on dark green base. The symptoms are observed on younger leaves and not on older leaves. No marginal or tip scorching is seen.

1.4.9 Zinc

Zinc is an essential micronutrient for biological systems. One of the critical physiological roles of Zn in biological systems is its role in protein synthesis and metabolism. Zinc is absorbed by plants as Zn^{2+}. The concentration of zinc in plants varies from 25 to 150 mg kg^{-1} of dry matter. In biological systems Zn is required by largest number of proteins. It has been estimated that nearly 2800 human proteins are capable of binding Zn which corresponds to 10% of human proteome (Andreini et al. 2006).

1.4.9.1 Uptake and Assimilation

Zinc is translocated from roots to shoots in the form in which it is taken up (Zn^{2+}). From the studies, various researchers have concluded that Zn is phloem mobile.

1.4.9.2 Physiological Functions

- Zinc is an important constituent of enzymes for protein synthesis. More than 300 enzymes contain Zn as its essential catalytic component. The major three enzymes containing Zn include carbonic anhydrase, alcoholic dehydrogenase and superoxide dismutase (Rattan 2015). These enzymes perform the following functions.

  1. Carbonic anhydrase (CA): presents in the cytoplasm, it facilitates the transfer of carbon dioxide or bicarbonates CO_2 fixation in photosynthesis. This forms the “limiting enzyme” for CO_2 fixation in C4 plants.
  2. Alcoholic dehydrogenase (AD): the conversion of acetaldehyde to ethanol is catalysed by this enzyme in anaerobic root respiration.
  3. Superoxide dismutase (SOD): the Zn-Cu-SOD protects the lipids and proteins of the membranes against oxidation by detoxifying superoxide radicals.

- Zn-containing enzymes are taking part in the regulation of RNA processing, translation and DNA transcription (Hansch and Mendel 2009).
- Zinc promotes synthesis of cytochrome C, and Zn plays an inevitable role in the N as well as carbohydrate metabolism of plants. The transport and translocation of phosphorus also are influenced by Zn (Rattan 2015).
- Zinc is required in seed development (Hansch and Mendel 2009).

1.4.9.3 Deficiency Symptoms

Zinc deficiency appears in the plants when the concentration falls below 15 mg Zn kg^{-1} of dry matter.

- Zinc deficiency is characterized by interveinal chlorosis and shortened internodes.
- Young shoots produce small leaves which are stiff in the case of Zn deficiency. These little leaves get malformed giving a bushy rosette appearance (Mengel and Kirkby 2006).
- A delay in maturity is observed in plants with Zn deficiency with stunted growth and a reduction in crop yield.

  The common Zn deficiency symptoms are:

  (i) Khaira disease in rice
  (ii) White bud of maize
  (iii) Little leaf of cotton
  (iv) Mottle leaf or frenching of citrus
  (v) Rosette disease of apple
  (vi) Crown choking in areca nut

- In coconut palms, button shedding along with the shortening of the crown is the reported symptom of zinc deficiency. There is a reduction in size of the leaf almost to its half with the shortage of Zn supply. Chlorosis is observed in leaflets which also appear narrower and shorter than normal. Flowering is affected in cases of acute Zn deficiency (TNAU 2015).
- In areca palm, crown choking happens in the initial stages with leaves turning dark green in colour. A reduction in the size of the leaves is also noticed with Zn deficiency.

1.4.9.4 Toxicity Symptoms

Zinc, when excess, limits growth of root and expansion of leaves. The Zn toxicity is characterized by chlorosis of leaves.

1.4.10 Copper

Copper is taken up mostly in the form of Cu^{2+} by roots. Two oxidation states of copper are Cu^{+} and Cu^{2+}. It interchanges between these two ionic forms as the monovalent form (Cu^{+}) is unstable (Hansch and Mendel 2009). A concentration of 5–30 mg Cu kg^{-1} of dry matter is considered to be the range of Cu in copper-sufficient plants (Rattan 2015).

1.4.10.1 Uptake and Assimilation

Copper uptake is considered as a process that is metabolically mediated. Copper as Cu^{2+} can be transported from older to newer leaves, though it is relatively immobile in plants.

1.4.10.2 Physiological Functions

- Copper plays an indispensable role in processes like mitochondrial respiration and photosynthesis. In the metabolism of carbon and nitrogen and in protection against oxidative stress, Cu is essential. It is also essential in carrying out cellular tasks. For example, synthesis of cell wall requires Cu (Hansch and Mendel 2009).
- Copper functions as reducing and oxidizing agent in biochemical reactions.
- Copper is an important component of enzymes like diamine oxidases, cytochrome C oxidase, polyphenol oxidase, ascorbate oxidase, superoxide dismutase (Cu-Zn-SOD), etc.
- Copper imparts resistance to plant diseases, and the fertility of male flowers is enhanced by copper.

1.4.10.3 Deficiency Symptoms

When the concentration of Cu in plants falls below 5 mg kg^{-1}, those plants are considered as copper deficient.

- Copper deficiency appears as necrosis, developing as spots at the tips of younger leaves, later extending along the margins towards the base of the leaf. Growth of the internodes becomes depressed. Malformation of leaves is observed later leading to premature abscission under severe Cu deficiency (Taiz and Zeiger 2002). The characteristic symptoms include necrosis, white tips, die back and reclamation disease.
- Copper deficiency results in the sterility of male flowers. It also delays the flowering and senescence is also resulted.

1.4.10.4 Toxicity Symptoms

Most commonly observed symptom of Cu toxicity is chlorosis, superficially resembling Fe deficiency. Another effect is on the inhibition of root growth.

1.4.11 Boron

The element boron is unique among the essential elements as the range in its concentration is very narrow between deficiency and toxicity. Soils contain 0.5–2 ppm of available B, but this constitutes only a part of the total B in the soil available to plants. Soil organic matter is the storehouse of B (Kelling 1999). Normal B-sufficient plants have B concentration ranging from 10 to 200 mg kg^{-1} of B (Rattan 2015).

1.4.11.1 Uptake and Assimilation

Boron is taken up as boric acid. Boric acid is the form of B that is potentially permeable to plant cells. Boron is considered to be phloem mobile for a large range of agricultural crops and is transported as a complex with polyols (primary photosynthetic product). Boron is immobile in plants.

1.4.11.2 Physiological Functions

- Boron is involved in the processes of respiration, synthesis of proteins, transport of sugars and metabolism of RNA, carbohydrate and plant hormones like indole acetic acid (Hansch and Mendel 2009).
- Boron plays a noticeable role in synthesis of cell wall and its lignification and cell wall structure. Boron helps in maintaining the structural integrity of biomembranes (Hansch and Mendel 2009).
- Chlorine and phosphorus transport is facilitated by boron, and it is also involved in the Ca nutrition in plants (Hansch and Mendel 2009).
- Production and retention of flowers, growth and elongation of pollen tube, pollen germination and development of seed and fruit require boron (Rattan 2015).
- Boron is essential for the growing tips of plants, as root tips, and new leaf and also helps in bud development. This helps in the transport of water, nutrients and sugars towards the actively growing regions of plants by maintaining healthy storage and conductive tissues. Boron assists in root growth by providing sugars needed for root development. This is also involved in ensuring normal development of root nodules in legumes, such as soybeans, alfalfa and peanuts (Rattan 2015).

Fig. 1.9 B deficiency in coconut. (Photo: T.K. Broschat)

1.4.11.3 Deficiency Symptoms

Soils with pH of 7.0 or above are more deficient in B than acid soils. When the B concentration in plants is of the order 5–30 mg kg^{-1}, plants are B deficient. B deficiency range varies from 5–10 mg kg^{-1} in graminaceous plants to 20–70 mg kg^{-1} in most of the dicotyledonous plants (Rattan 2015). Boron deficiency symptoms appear initially in the younger leaves as well as growing tips at the apex as B is relatively immobile in the plants. The leaves may get malformed and appear bluish green in colour. The internodes become shorter giving a rosette appearance as boron deficiency damages actively growing organs such as tips of shoots and roots. The deficiency results in stunting of the whole plant.

- Retention of flowers, formation of pollen, elongation and growth of pollen tube, germination, fixation of nitrogen and assimilation of nitrates are adversely affected due to B deficiency.
- In citrus fruits, uneven thickness of the peel, lumpy fruits and gummy deposits result due to B deficiency.
- In coconut palm, B deficiency is widely noticed. The symptoms include shortened, crinkling of the unfolding leaflets (Broschat 2009; Fig. 1.9). In more advanced stages, terminal leaflets remain fused. The tips of these leaflets may be "knife shaped", with or without a brown solution oozing out through the hook. This symptom is also called "hookleaf" (Broschat 2009; Fig. 1.10). The basal part of the petiole may be without leaflets. In adult palms, the deficiency leads to production of branched spikes, premature death of inflorescence, production of inflorescence with lesser female flowers and shedding of buttons (female flowers). Other associated symptoms include "hen and chicken" symptom (a few underdeveloped nuts/small-sized nuts along with full developed nuts), cracking of nuts externally/internally with meat protruding towards the mesocarp and barren nuts with partial/unevenly developed kernel having poor-quality copra. Pollen production, pollen grain germination and pollen tube development will be

Fig. 1.10 B deficiency in coconut. (Photo: T.K.Broschat)

affected. Often, the malformations may be exhibited either singly or by various combinations based on the intensity of the deficiency. Drought may aggravate boron deficiency and in some cases seasonal boron deficiency, i.e. the symptoms appearing in the dry season and disappearing in the wet season could be noticed.

- The breakdown of internal tissues of root crops appears as darkened areas and is referred as brown heart or black heart.
- Common boron deficiency symptoms include:

  1. Internal cork of apple
  2. Top sickness of tobacco
  3. Crown rot/heart rot in sugar beet
  4. Browning and hollow stem of cauliflower
  5. Cracked stem of celery

1.4.11.4 Toxicity Symptoms

If the levels of B exceeds even slightly than the critical range, B toxicity occurs in majority of the crops. Boron toxicity occurs mostly in arid and semiarid region soils with high concentration of B. More than 5.0 ppm available boron is considered toxic to many agronomic crops (Kelling 1999).

- The major B toxicity symptoms begin as yellowing of leaf tips which later progresses leading to necrosis of leaf. This ends up in scorching of leaves and premature dropping (Mengel and Kirkby 2006). Some plants may also develop black spots on older foliage.

1.4.12 Molybdenum

Molybdenum in soil is predominantly determined by total Mo content in the soil and the soil reaction as measured by soil pH. Molybdenum is taken up by plants as molybdate (MoO_4^{2-}) ions. Molybdenum exists in three valence states of Mo (IV), Mo (V) and Mo (VI). This property imparts its biochemical role.

1.4.12.1 Uptake and Assimilation

Translocation of molybdate across the plasmalemma is facilitated by phosphate binding and transport sites, though it is not clear in which form it is translocated (Heuwinkel et al. 1992).

1.4.12.2 Physiological Functions

- Plant proteins involved in the assimilation of nitrogen, metabolism of sulphur, stress reactions and biosynthesis of phytohormone contain Mo. Molybdenum is involved in mechanism of nitrogen assimilation especially in nitrate reductase and nitrogenase enzymes. The key enzyme involved in nitrogen assimilation is nitrate reductase (brings about the reduction of nitrate to nitrite) whereas nitrogenase is involved in nitrogen fixation (Hansch and Mendel 2009). Molybdenum is a structural component of nitrogenase enzyme, and it consists of a Mo-Fe-S protein and a Fe-S cluster protein which are metalloenzyme proteins.
- In the abscisic acid biosynthesis, Mo-containing enzyme aldehyde oxidase is involved in the last step of catalytic reactions. Sulphur oxidase, another enzyme which contains Mo, helps in protecting the plants against the harmful effects of sulphite, resulting from acid rain (Hansch and Mendel 2009).
- Molybdenum affects the activities of enzymes like alanine aminotransferase and ribonuclease involved in biosynthesis of proteins. Pollen formation, its viability and anther development are also influenced by Mo.

1.4.12.3 Deficiency Symptoms

Molybdenum concentration in Mo-sufficient plants ranges between 0.1 and 2 mg kg^{-1}. When this falls below 0.1 mg kg^{-1}, deficiency occurs. Deficiency symptoms in young plants include mottling, leaf cupping, grey tinting and flaccid leaves which are often found on seedlings that remain dwarfed until dying (Hewitt and Bolle-Jones 1952a). Sometimes in older plants, where deficiencies have been corrected or when deficiency levels are modest, the symptoms appear in younger leaf tissues with the characteristic loss of proper lamina development (whip-tail), leathery leaves and meristem necrosis (Hewitt and Bolle-Jones 1952b). Molybdenum deficiency resembles N deficiency. As Mo is readily translocated within plants, the symptoms initially appear in older or middle leaves.

- Molybdenum deficiency is characterized by interveinal chlorosis and necrosis appearing initially on the older leaves. The typical symptoms develop as upward curling of leaf margins. The twisting of leaves with no necrosis is particularly observed in cauliflower/broccoli and is termed as the whiptail disease. Eventually the leaves die. The formation of flowers is hindered, and premature abscission of flowers is also observed in this case.
- In legumes, Mo deficiency impairs nitrate reduction and nitrogen fixation. This in turn results in a N deficiency in the affected crop.

1.4.12.4 Toxicity Symptoms

Higher concentration of molybdenum in foliage results when these crops are grown in soils with higher concentration of molybdenum. When cattle and sheep are fed on such foliage, a diseased condition known as molybdenosis results.

1.4.13 Nickel

Nickel was recognized as essential in the year 1987, i.e. the most recently discovered micronutrient. The Ni requirement by plants is low as <0.5 mg kg^{-1}. Nickel is taken up by plants as Ni^{2+} ions. In plants, it exists in three oxidation states, I, II and III (Hansch and Mendel 2009). Nickel is a key component of selected enzymes involved in N metabolism and biological N fixation in crops.

1.4.13.1 Uptake and Assimilation

Two nickel transport systems inside plants are explained by Brown (2006) which include low-affinity transport system and high-affinity transport system. As the name suggests, the low-affinity transport system absorbs lower concentration, and high-affinity transport system absorbs higher concentration of Ni^{2+} ions which, respectively, being 4.4 ppb (0.6 ounces Ni per million gallons of water) and 1.8 ppm (237.7 ounces Ni per million gallons of water). Nickel ions are easily transported within the plant. Due to this reason, Ni from shoots is transported to seeds, which could be accounted to 70% of Ni present in the shoots (Brown 2006).

1.4.13.2 Physiological Functions

- In a number of prokaryotic enzymes like hydrogenases, dehydrogenases and methyl reductases, Ni is found essential (Hansch and Mendel 2009).
- Urease enzyme contains Ni and this enzyme is essential in N metabolism in plants. Nickel acts as a cofactor in plant urease aiding the hydrolysis of substrate (urea) to carbon dioxide and ammonia (Liu et al. 2014). In germination of seeds, urease plays an important role (Seregin and Kozhevnikova 2006).
- In certain legumes, for the growth of root nodules and activation of enzyme hydrogenase, Ni is required (Seregin and Kozhevnikova 2006). Activity of hydrogenase enzyme is optimized with adequate supply of Ni in the case of free-living *Rhizobium.*
- Nutrient transport to seeds or grains is supported by the presence of Ni.

1.4.13.3 Deficiency Symptoms

Typical nickel deficiency symptoms have not been defined adequately. A reduction in the urease activity would result in the accumulation of toxic urea. This is resulting from Ni deficiency as the absence of Ni adversely affects the hydrolysis of urea to carbon dioxide and ammonia.

Essentiality of Ni was first established in the year 1987 when a deficiency was noticed in barley. In barley it was observed as the inability to produce viable seeds due to poor embryo growth. This was observed as poor or underdevelopment of the embryonic root. Reduction in dehydrogenase activity and poor development of endosperm were also reported (Seregin and Kozhevnikova 2006). The critical Ni concentration in barley tissues that reduced the yield by 15% was 0.1 mg kg^{-1} of dry matter.

- Reduction in dry matter weight, decrease in amino acid content and accumulation of nitrates are few symptoms of Ni deficiency.
- Leaf tip necrosis is the major symptom of Ni deficiency. In cowpea, the deficiency symptoms include leaf tip necrosis and leaf chlorosis (Rattan 2015).
- Ni-deficient pecans develop a particular deficiency symptom in leaves known as “mouse-ear” leaves (Fig. 1.11). There occurs a delay in the leaf expansion on branches of Ni-deficient pecans as a result of Ni deficiency. It also decreases bud break. Rosetting, bronzing, tip necrosis and chlorosis are the common symptoms observed on the leaves (Liu et al. 2014).

1.4.13.4 Toxicity Symptoms

Soil is the major source of Ni to plants. Soil conditions affect nickel availability, and it is higher in over-moistened soils7 of low humus content and soils with light granulometric composition. Soil reaction also plays an important role in availability of

Fig. 1.11 Mouse ear in pecan – nickel deficiency (Source: http://extension.uga.edu/publications/detail.cfm?number=B1304)

Ni. Low pH of the soil solution enhances, and higher pH declines accessibility of Ni by plant roots (Seregin and Kozhevnikova 2006). Higher Ni concentration may turn toxic to plants.

- Excess of nickel decreases plant transpiration, moisture content and stomatal conductance.
- Toxic concentrations of nickel decrease the size and number of chlorophyll and its synthesis resulting in reduced rates of photosynthesis. The activities of enzymes involved in Calvin cycle are also adversely affected with an excess of Ni content (Seregin and Kozhevnikova 2006).
- Nickel toxicity inhibits plant growth. Several species accumulate Ni in their roots and are known as the excluder species. In these, inhibition of root growth is severe than shoot growth in case of Ni toxicity (Seregin and Kozhevnikova 2006).
- Symptoms of Ni toxicity include chlorosis in leaves. In cereals, the symptoms appear initially as yellowish stripes along the leaves. This later results in turning the entire leaf whitish, and leaf margin necrosis develops at extremely toxic conditions. Interveinal chlorosis in the leaves is observed as Ni toxicity symptom in the case of dicotyledonous crops, which resembles the symptoms of Mn deficiency (Mengel and Kirkby 2006).

1.4.14 Chlorine

Chlorine absorbed as Cl^- ions by plants is the most mobile nutrient in the soil and hence gets easily leached under freely drained conditions. In healthy plants, its concentration ranges from 100 to 500 mg kg^{-1} of dry matter. Chloride is a mobile anion in plants.

1.4.14.1 Uptake and Assimilation

Chlorine uptake occurs against an electrochemical gradient permeably mediated by a Cl^-/H^+ cotransport across the plasmalemma because low pH promotes Cl^- uptake. This proves that Cl^- uptake is metabolically controlled.

1.4.14.2 Physiological Functions

- The major function of Cl^- is in the maintenance of electrical charge balance and osmoregulation. This is involved in the opening and closure of stomata.
- Chlorine plays a major role in photosynthesis. It acts as a cofactor in the oxygen-evolving complex and thus forms a structural constituent of photosystem II (Kusunoki 2007).
- Chlorine imparts resistance to plant diseases in plants, viz. stem rot and sheath blight in rice, *Fusarium* root rot in barley, common root rot in barley, stalk rot in corn, grey leaf spot in coconut palms, common root rot and take-all disease in wheat, downy mildew in millet, hollow heart and brown centre in potatoes and *Fusarium* yellows in celery.

1.4.14.3 Deficiency Symptoms

Chlorine is highly soluble and therefore can leach away from sandy soils in heavy rainfall areas and would lead to chlorine deficiencies. However, Cl deficiency has not been reported in India, attributed to the abundance of chlorine in air and addition of Cl^- ions through different fertilizer carriers like muriate of potash and ammonium chloride (Mengel and Kirkby 2006). When the concentration of Cl^- in plants is less than 100 mg kg^{-1}, plants are designated as Cl deficient.

- Chlorine deficiency symptoms include chlorosis of leaves, curling of leaves, decrease in leaf surface area, restricted branching of root systems and plant wilting (Hansch and Mendel 2009). Few of these symptoms like leaf wilting and chlorosis resemble those of Mn deficiency.
- Characteristic Cl deficiency symptom is leaf wilting along the margins as transpiration is adversely affected with Cl deficiency and the plants remain chlorotic (Mengel and Kirkby 2006).

1.4.14.4 Toxicity Symptoms

Excess of Cl^- ions in plants causes chlorine toxicity, and it is commonly observed in salt-affected soils. The symptoms of chlorine toxicity include leaf tip or margin burning, bronzing, premature yellowing and abscission of leaves, resulting in reduction in yield and quality in the later stages (Mengel and Kirkby 2006).

1.4.15 Silicon

Silicon is available to plants mostly in the form of monosilicic acid – $Si(OH)_4$. Silicon was found essential to horsetail (*Equisetum arvense*) and wetland paddy (*Oryza sativa*) till date (Chen and Lewin 1969; Richmond and Sussman 2003). As a deficiency in silicon can negatively affect normal growth and development in a plant, silicon could be adjudged as an element "quasi-essential" to plants.

1.4.15.1 Uptake and Assimilation

Silicon is taken up by plants in the form of silicic acid though the mechanism of uptake is still not clear. Plants take up Si in the form of silicic acid, which is transported to the shoot, and after loss of water, it is polymerized as silica gel on the surface of leaves and stems. Evidence is lacking concerning the physiological role of Si in plant metabolism (Ma et al. 2001).

1.4.15.2 Physiological Functions

- Silicon is accumulated in the cell walls mainly as amorphous silica ($SiO_2.nH_2O$). This contributes to enhanced rigidity and strength of cell wall as the amorphous silica combines with pectins and polyphenols present in the cell wall.
- Silicon helps in preventing stress due to abiotic factors in plants (Pilon-Smits et al. 2009). Silicon can ameliorate the toxicity due to heavy metals. The abiotic stresses developed due to UV radiation, imbalances in nutrients, salt levels and temperature can be alleviated by Si. Enhancement of sodium exclusion and a reduction in lipid membrane peroxidation have favoured mitigating stress due to salinity reasons according to a study by Saqib et al. (2009).
- Silicon reduces susceptibility of plants to fungal diseases and thus helps in improving the plant health. This could be either by preventing penetration of fungus to cell wall and thereby preventing the infection or by improving peroxidize, polyphenol oxidase and chitinase enzyme activities, by enhancing the antimicrobial compounds or phenolic compounds production (Pilon-Smits et al. 2009).

1.4.15.3 Deficiency Symptoms

- Growth and development of plants and reproduction are adversely affected with the deficiency of Si. Infections due to fungal attacks and decreased resistance to lodging are more common in case of plants deficient in silicon**.**

1.5 Growth Laws

1.5.1 Liebig's Law of the Minimum

The role of nutrients in the plant growth is explained using this law. This law gives emphasis on the nutrient which is present in its minimum, which actually regulates the growth. Justus von Liebig (1840) in the law observes that "every field contains a maximum of one or more and a minimum of one or more nutrients. With this minimum, be it lime, potash, nitrogen, phosphoric acid, magnesia or any other nutrient, the yields stand in direct relation. It is the factor that governs and controls yields. Should this minimum be lime yield will remain the same and be no greater even though the amount of potash, silica, phosphoric acid, etc. be increased a hundred fold". This was later simplified as Liebig's law of the minimum. This states that "Even if all but one of the essential possible elements be present, the absence of that one will render the crop barren" (Salisbury 1992). Thus the law states the importance of the limiting nutrient in the plant nutrition. This was well explained using the broken barrel concept, in which the capacity of a barrel with staves of unequal length is limited by the shortest stave, which in a similar way, a plant's growth is limited by the nutrient in shortest supply (Fig. 1.12). This nutrient is referred as the growth-limiting nutrient. Thus only by improving the availability of the least abundant nutrient, growth can be improved. The law predicts that when the nutrient in the minimum (X) is added in increasing amounts to a plant, correspondingly increasing yields (Y) are obtained until a second nutrient comes in to be the minimum.

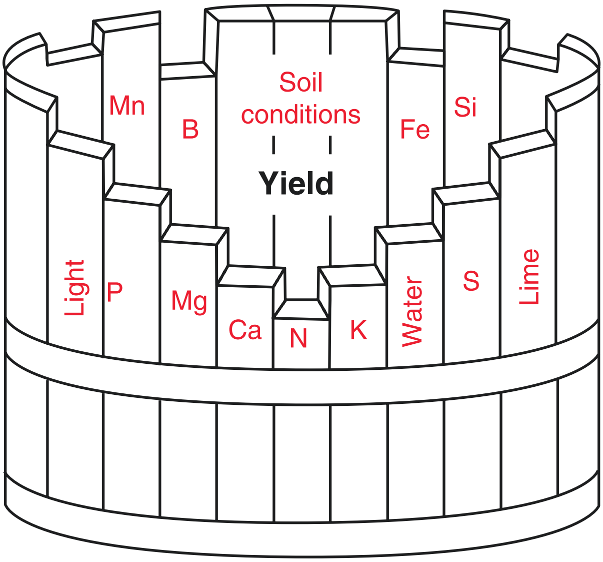

Fig. 1.12 Liebig's law of minimum – broken barrel analogy

1.5.2 Mitscherlich's Laws

E.A. Mitscherlich quantified the relationship between yield and growth factors. The two laws given by him are:

1. *Mitscherlich's law of physiological relationship*: This states that yield can be increased by each single growth factor even when it is not present in the minimum as long as it is not present in the optimum.
2. *Mitscherlich's growth law*: Increase in yield of a crop as a result of increasing a single growth factor is proportional to the decrement from the maximum yield obtainable by increasing that particular growth factor.

Mitscherlich observed that when plants were supplied with adequate amounts of all but one nutrient, their growth was proportional to the amount of this one limiting nutrient that was supplied to the soil. Further plant growth increased as the more amount of this nutrient was added, but the increase in growth with each successive addition of this element was progressively smaller. Mitscherlich (1909) developed a mathematical equation relating yield to the supply of plant nutrients. The equation is as follows:

$$dy / dx = (A - y)c \text{ or } (1 / A - y).dy / dx = c$$

where

dy/dx = increase in yield associated with dx increment in a specific fertilizer nutrient
A = maximum potential or attainable yield when all the nutrients are supplied or are present in the optimum amounts
$\underline{c}$ = constant, which is the efficiency factor

Upon integration, the above equation assumes the form of

$$\log (A - y) = \mathrm{K} - cx$$

where K = constant

1.5.3 Law of Maximum

This principle was developed by Arthur Wallace in 1993. The Law of the Maximum does not hold good if there are any Liebig-type limiting factors present. It has two major characteristics. First, the effect of a given input is progressively magnified as other limiting factors are corrected. The final result is greater than the sum of the effects of the individual inputs because of the way in which they interact. The interaction multiplies the effects of each. Second, yields can be highest or maximum only if there are no remaining limiting factors; the fewer limiting factors that remain, the higher will be the yield. How closely this can be approached, of course, depends upon economics. Fortunately, when dealing with Mitscherlich-type factors, those most economical to use can be chosen first (Wallace and Wallace 1993).The law states that “when the need is fully satisfied for every factor required in the process, the rate of process can be at its maximum potential, which is greater than the sum of the individual parts because of the sequentially additive interactions”. This is based on the philosophy of synergistic interactions.

1.6 Bray’s Concept of Nutrient Availability and Mobility

Nutrient availability involves several factors like the nature of soil nutrients, soil conditions and plant root relations by which plant metabolism happens. Roger H. Bray in 1938 proposed that the “soil available nutrient is that fraction of total amount whose variation in amount is responsible for significant changes in yield and response; further, the availability of these soil forms, however, involves not only their chemical and physical nature but also the ability of the plant to “forage” them with its root system” (Bray 1938).

The concept of nutrient mobility was introduced by Bray in the year 1954. He explained mobility as the “overall process whereby nutrients reach the sorbing root surfaces, thereby making possible their sorption into the plant” (Bray 1954). This, on the whole, describes the movement of nutrients in the soil towards root surface or the movement involved in the soil solution or exchange of the nutrient. Soil colloids are negatively charged. Hence, positively charged ions (cations like NH_4^+, K^+, Ca^{2+}, Mg^{2+}, Fe^{2+} or Fe^{3+}, Mn^{2+}, Zn^{2+}, Cu^{2+}, Ni^{2+}) are strongly held on to the soil colloidal surface as exchangeable cations or are specifically adsorbed. Whereas, the anions negatively charged are not adsorbed by the solid phase. These anions like Cl^-, NO_3^-, SO_4^{2-}, $BO_3^{3-}/HBO_3^{2-}/H_2BO_3^-$ and HCO_3^- remain in soil solution and are easily mobile in the soil solution. Phosphate (PO_4^{3-}) and molybdate (MoO_4^{2-}) ions, though anions, are held in the soil by anion exchange or ligand exchange mechanisms. These are adsorbed or precipitated as sparingly soluble phosphates of Fe, Al, Ca, etc. depending on the soil reaction.

Nutrients should come in touch with the surface of roots to become available to the plants. When the nutrients are held in solid phases as exchangeable or labile forms, these are easily available for absorption by plant roots in comparison to the nutrients in solution. But the farther these ions are from absorbing root surfaces, the more is the time taken for adsorption by plant roots, which is indicated using the term “immobile” nutrients.

The classification of nutrients into mobile and immobile forms as given by Bray (1954) is represented in Table 1.3 and illustrated in Fig. 1.13.

Table 1.3 Classification of mobile and immobile nutrients

Plant		Soil	
Mobile	Immobile	Mobile	Immobile
Cl	B	$H_3BO_3/H_2BO_3^-$	NH_4^+
Mg	Ca	Cl-	Ca^{2+}
Mo	Cu	NO_3^-	Mg^{2+}
N	Fe	SO_4^{2-}	Fe^{2+} or Fe^{3+}
K	Mn		PO_4^{3-}
	Zn		MoO_4^{2-}
	S		Ni^{2+}
			K^+

Source: Rattan and Goswami (2009)

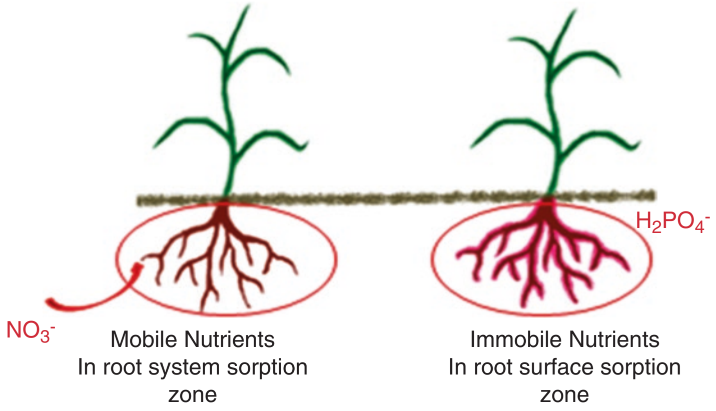

Fig. 1.13 Bray's nutrient availability concept

1.7 Mechanisms of Nutrient Transport

Certain mechanisms exist for the movement of nutrients from soil to roots. These include three distinct processes, viz. mass flow, diffusion and root interception. These mechanisms are diagrammatically represented in Fig. 1.14.

1.7.1 Mass Flow

Mass flow is described as the movement of nutrients along with the movement of water in the soil towards the root surface as a result of transpiration-induced convective water flow. Mass flow gets decreased with a decrease in water content in soil as mass flow depends on the rate of water flow towards the root surface.The amount of nutrient supplied by mass flow may be calculated by using the equation

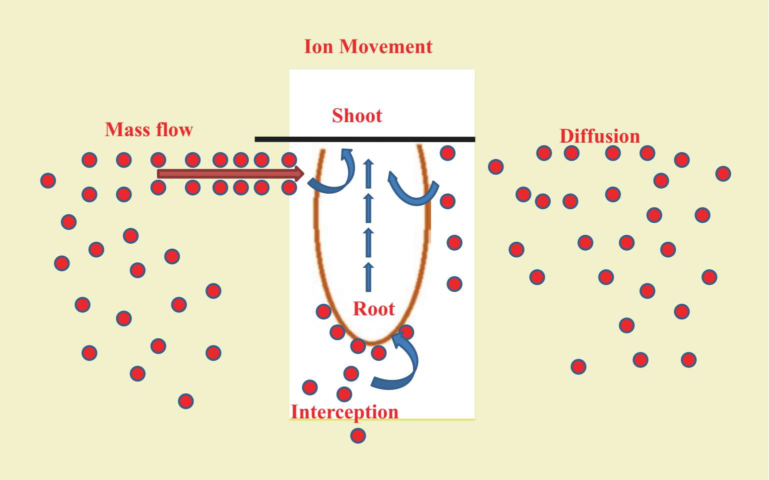

Fig. 1.14 Mass flow, diffusion and root interception

$$J = v \times C_1$$

where

J = nutrient supplied
v = amount of water transpired during the cropping season to produce the given dry matter(y)
C_1 = average concentration of the nutrient ion in bulk soil solution

Amount of water used by crop during the season is computed using either transpiration ratio or amount of water used by the crop. Essential nutrients like N, Ca, Mg, S, Cu, B, Mn and Mo are mainly moved towards the root by the method of mass flow.

1.7.1.1 Factors Affecting Mass Flow

(a) Soil water content: Mass flow decreases as the soil water content decreases.
(b) Temperature: As the temperature decreases, mass flow decreases. This is due to the reduced transpiration rate as well as movement of water due to lower temperature.
(c) Size of the root system: This affects the uptake of water and nutrients moving along with water. In the case of nutrient movement by mass flow, root density is less critical than by diffusion and root interception (Rattan 2015).

1.7.2 *Diffusion*

The process of diffusion takes place based on a concentration gradient. In diffusion, ion moves from a higher concentration to a lower concentration. When the concentration of a particular ion at the root surface is decreased, the movement of ions towards the roots increases and vice versa. Diffusion occurs based on Fick's law, which is given by the equation

$$F = -D\ dc / dx$$

where

F = diffusion rate (quantity diffused per unit cross section per unit time)
dc/dx = concentration gradient
c = concentration
D = diffusion gradient
x = distance

This law states that the amount of nutrient ions moving/diffusing per unit area per unit time is proportional to concentration gradient. Essential nutrients like P, K, Zn and Fe are mainly transported by diffusion to the root surface. In comparison to the mass flow, diffusion is a slow process for the movement of nutrients to the roots.

1.7.2.1 Factors Affecting Diffusion

(a) Soil water: Since diffusion of nutrient ions needs water, soil water has a major role in the movement of nutrient ions by diffusion. Diffusion reduces in case the moisture content becomes less in soil.

(b) Soil compaction: Soil compaction results in bringing the soil particles closer by exclusion of air, and the continuity of moisture flows decreases. This in turn results in decreased diffusion rate of nutrients to roots.

(c) Temperature: Lower temperatures reduce diffusion as ions need minimum activation energy for enabling them to participate in the reaction. Rise in temperature in addition to overcoming this activation energy step increases fluidity or reduces the viscosity of water. This in turn facilitates the diffusion of ions.

(d) Chemical amendments: The addition of amendments to soil like lime, gypsum, etc. results in a change in the ionic concentration in the soil solution. For example, a rise in pH associated with lime decreases the concentration of cations and increases the concentration of anions in soil solution. This results in increased diffusion of anions and decreased diffusion of cations to roots from soil. Addition of gypsum reduces the pH in sodic soil, as a result of which, the effective diffusion coefficient rises. Added organic manures release low molecular weight biochemicals which forms soluble organometallic complexes with the cations. This complexation causes reduction in buffer power and increase in the effective diffusion coefficient values (Rattan 2015).

1.7.3 Root Interception

Root interception is the process in which the nutrients come in direct physical contact with the surface of roots. Mass and surface area of roots are deciding factors in the process of root interception. The larger the mass and surface area, the larger the nutrient supply as it enables the plant to explore from larger area in soil. The root volume thus plays a significant role in the quantity of nutrient supply to the plants. Mycorrhizal fungi colonize the roots and thereby favour root exploration to a greater extent. This enhances root interception. The nutrient which is mainly taken up by root interception is calcium. Magnesium, Zn and Mn in lesser amounts follow root interception. Factors which restrict growth of roots like compaction, dryness of soil, soil acidity, restricted aeration, root diseases including insect attacks, nematode infection and abnormally high or low soil temperature reduce the contribution of root interception (Rattan 2015).

1.8 Nutrient Uptake into the Root and Plant Cells

The extent of complexity in plant-soil-atmosphere relationships brings in the involvement of scientists belonging to different technical backgrounds when it comes to plant nutritional physiology. Nutrient uptake by plants can be addressed at two stages – uptake by roots from the rhizosphere along with water and subsequent uptake and transport in the plant system. Initial absorption of water and nutrients by plant roots is essential for their incorporation into plants.

1.8.1 Uptake of Water and Nutrients by Roots

Movement of water towards roots is mainly driven by capillary action and osmosis. In roots, root hairs are present which facilitate the uptake of water and nutrients from soil by increasing the root surface area. The surface area of contact is deterministic of water uptake potential and is maximum as much as the root and its hairs spread into the rhizosphere (Taiz and Zeiger 2002).

Water entry into the root is defined by the root hair zone and subsequently thereafter by two important regions called exodermis (mature outer layer of protective tissue) and hypodermis (hydrophobic layer relatively impermeable to water). Soil water contains nutrients in dissolved form which can be called as solutes. Osmosis occurs as soil water movement from a lower solute concentration to a higher solute concentration.

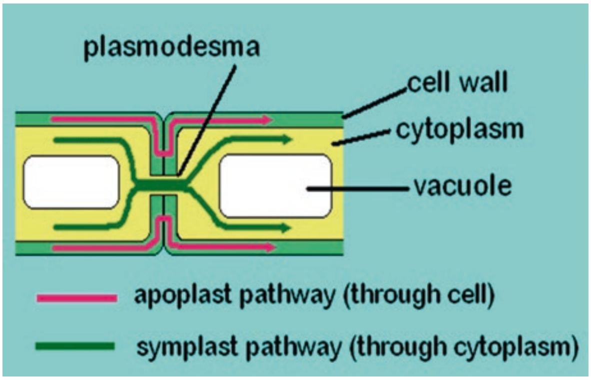

Fig. 1.15 Apoplast and symplast pathways (Source: https://upload.wikimedia.org/wikibooks/en/0/00/Waterpathwaysthroughrootcells.gif)

1.8.1.1 Apoplast, Transmembrane and Symplast Pathways

Water is transported mainly by bulk flow in the soil. Once the bulk flow reaches the root surface, from the root epidermis to the endodermis, there are three major modules of water flow which are as follows:

1. Apoplast pathway: Water movement occurs only through cell wall and the intercellular air spaces in plant tissues, without passing through any membranes.
2. Transmembrane pathway: Water moves across plasma membranes of adjacent cells in a sequential manner.
3. Symplast pathway: Water movement occurs from one cell to the next via the plasmodesmata also consisting of the interconnected cell cytoplasm.

The apoplast and symplast pathways are represented in Fig. 1.15.

At the endodermis, Casparian strips appear as the first physical barrier for the apoplastic movement of water and solutes. Casparian strip is a band of radial cell walls in the endodermis with suberin deposits, which are waxlike and hydrophobic in nature. Casparian strips force water and solutes in the apoplastic region to cross the endodermis by passing through the plasma membrane. The cortex (towards outside) and stele (towards inside) are separated by the radially suberized endodermis. The plant vasculature is systematically arranged in the stele which consists of xylem (water and solute transport from root to shoot) and phloem (metabolite and assimilate transport from shoot to root and other parts).

1.8.1.2 Uptake of Nutrient Ions

Diffusion and cation exchange are the two mechanisms by which nutrients move towards the plant root. Diffusion takes place on a concentration gradient. Cation exchange process occurs in response to the release of a hydrogen ion from the plant

Table 1.4 Different areas of roots for nutrient absorption

Sl. No.	Crop	Nutrient	Area of absorption	Reference
1	Barley	Calcium	Root apical region	Clarkson (1985)
2	Barley	Iron	Root apical region	Clarkson (1985)
3	Corn	Iron	Entire root surface	Kashirad et al. (1973)
4	Several crops	Potassium, nitrate, ammonium and phosphate	Entire root surface	Clarkson (1985)
5	Corn	Potassium accumulation	Root elongation zone	Sharp et al. (1990)
6	Corn	Nitrate absorption	Root elongation zone	Taylor and Bloom (1998)
7	Corn and rice	Ammonium	Root apical region	Colmer and Bloom (1998)
8	Several crops	Different ions	Apical regions of the root axes or branches	Bar-Yosef et al. (1972)
9	Several crops	Different ions	Entire root surface	Nye and Tinker (1977)

root, resulting in a change in the soil pH around the root vicinity. When these water and nutrient ions enter the plant root, they move through either apoplastic, trans-membrane or symplastic pathways and subsequently the capillary action allowing the upward movement of water. Subsequently transport of nutrients via xylem takes place.

There is a considerable diversity in the different areas of the roots that take up or absorb nutrients differentially. As has been reported in earlier studies, a few examples are tabulated in Table 1.4.

1.8.2 Absorption of Nutrients into Plant Cells

Plasma membrane and tonoplast act as barriers that selectively regulate the movement of water and nutrients into and out of the cell. These cell barriers are:

- Permeable to oxygen, carbon dioxide as well as certain compounds
- Semipermeable to water
- Selectively permeable to inorganic ions and organic compounds, such as amino acids and sugars

Nutrient ions may move across these barriers actively or passively.

1.8.2.1 Passive Transport

Passive transport takes place along a concentration gradient. Nutrients diffuse to the cell, when the concentration of a particular nutrient falls less inside the cell. This type of transport requires no energy, and the nutrient concentration is maintained for enhancing nutrient absorption (e.g. nitrate converted to ammonia to elicit more nitrate absorption). Passive transport involving absorption of ions without expenditure of energy is defined by three major theories of absorption:

(a) Ion exchange theory – This involves cation exchange theory (exchange of cations on soil clay with protons on root surface) and carbonic acid exchange theory (carbonic acid in soil dissociates into protons and bicarbonate ions, and these protons exchange with cations present on root surface; when continuous orbiting stops, exchange occurs).
(b) Donnan effect and equilibrium – Cell membrane has a negative charge which allows anions to enter. Plants can accumulate about 30 times the cations passively against concentration gradient to balance the electrochemical potential difference thus generated. At equilibrium defined by F. G. Donnan, the ratio of positively charged ions inside to outside will be equal to the negatively charged ions inside to outside.
(c) Mass flow – Due to active transpiration, ions are taken up from root to shoot xylem. This leads to a concentration gradient and a water pressure gradient which drives the mass flow.

1.8.2.2 Active Transport

Active transport happens against a concentration gradient. This type of movement involves energy. There are three major mechanisms for active absorption:

(a) ATP-mediated ATPase pumps – Here ions are actively absorbed by using energy released by hydrolysis of ATP, e.g. H^+ ATPase pumps.
(b) Cytochrome pumps – Whenever a tissue is placed in a salt solution, the associated respiratory increase is called salt respiration which is mediated by iron-containing membrane proteins called cytochromes. Protons and electrons are produced due to dehydrogenation reaction in the inner side of the impermeable membrane due to difference in oxygen concentration. The ferric ions on the outside of the membrane-bound cytochrome pumps accept an electron and get reduced, and subsequently the electron is transferred or carried outside by the cytochrome chain. This cycle repeats after the next anion is taken up by the ferric ion from outside. This concept was proposed by Lundegardh in 1954.
(c) Phospholipids as carriers, e.g. diacylglycerides like lecithins.

1.8.2.3 Membrane Transport

Membrane transport is mediated by specialized proteins which are described below:

1. Channels: These are transmembrane proteins that exist as membrane pores which selectively permit solutes based on its biochemical and biophysical properties. The entry of ions is determined by the layer of hydration, e.g. aquaporins.
2. Pumps: These are transmembrane proteins that transport ions actively by TP hydrolysis. Protons are pumped against electrochemical gradient which builds up a positive charge due to the protons accumulated.

   There are two types of active transport that occur.

   (a) Primary active transport – Here the energy from ATP hydrolysis is directly used for proton transport against concentration gradient thereby creating electrochemical potential gradient.
   (b) Secondary active transport – Due to the electrochemical potential gradient that is generated as a result of primary active transport, the protons pumped outside against the concentration gradient result in a chemical potential difference of about 10–100 times, which is used for absorption of other ions. There are two forms of secondary active transport.

       (i) Symport (cotransport) – Where proton moves along with another anion in the same direction
       (ii) Antiport (counter transport) – Where the energy generated due to the accumulation of protons is used for expelling cations, wherein the protons move inside and cations move outside

3. Carriers: This concept defines a specific carrier for each ion. Charged ions move through protein components across a membrane and not through the lipid part. The enzyme phosphokinase mediates the formation of an activated carrier (with a conformational change) which then accepts the ion to form the carrier-ion complex on the outside of the membrane. The carrier-ion complex gets energized and moves through the membrane along with the carrier. Enzyme phosphatase changes the conformation of the carrier-ion complex and releases the ion in the inner membrane.

A very small proportion of the total nutrient requirement is met by bulk flow, which reduces the diffusion rates when nutrient absorption by root exceeds the available concentration in the soil (Mengel and Kirkby 1987). This results in the formation of a nutrient depletion zone adjacent to the root surface, about 0.2–2.0 mm from the root surface. Optimal nutrient acquisition depends both on the capacity for nutrient uptake and on the ability of the root system to grow into fresh soil.

1.9 Conclusion

Essential nutrients enable proper plant growth by carrying out physiological functions. The availability of all these nutrients in soil fluctuates depending on many factors. This may vary resulting in deficiency or toxicity of nutrients. The deficiencies and toxicities of these nutrients lead to particular disorders which could be identified by the symptoms on plants and later by proper soil and plant analysis. The nutrients from the soil move towards the roots by following certain mechanisms of transport, which include mass flow, diffusion and root interception. The nutrients thus reaching the roots are absorbed by plants either actively by spending energy or passively by no involvement of energy.

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Chapter 2
Role of Plant Nutrients in Plant Growth and Physiology

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Abstract A mineral element is considered as essential based on the criteria of essentiality given by Arnon (Criteria of essentiality of inorganic micronutrients for plants. In: Wallace T Trace elements and plant physiology. Chronica Botanica, Waltham, pp 31–39, 1954), according to which 16 elements known as mineral nutrients are required for completion of a productive life cycle in plants. These mineral nutrients are carbon, hydrogen, oxygen, nitrogen, phosphorus, potassium, calcium, magnesium, sulphur, iron, manganese, zinc, copper, boron, molybdenum and chlorine. Of these C and at times S are taken up from air as CO_2 and SO_2, and oxygen and hydrogen are provided as water. The soil is the source for uptake of the other elements by plants. Based on their requirement, these nutrients have been classified as macronutrients (N, P, K, Ca, Mg and S) because they are required at concentrations higher than 1–150 g per kg of plant dry matter and micronutrients (Fe, Zn, Mn, Cu, B, Mo and Cl) which are required at concentration of 0.1–100 mg per kg of plant dry matter. However their requirement per se does not alter their significance for the plant growth and metabolism. The mineral nutrient elements play essential roles such as constituent of cell structures and cell metabolites, in cell osmotic relations and turgor-related processes, energy transfer reactions, enzyme-catalysed reactions and plant reproduction. Plant productivity depends on the efficient discharge of these functions. In this chapter we focus on the main functions of the mineral nutrients that have a bearing on the quantitative and qualitative aspects of crop productivity.

Keywords Essential · Micronutrient · Macronutrient · Physiological roles

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2.1 Introduction

Sixteen elements have so far been unequivocally shown to be essential for growth and development of higher plants as per the criteria of essentiality given by D. I. Arnon in 1954. The mineral nutrient elements play essential roles that can be broadly grouped as follows:

1. As constituent of cell structures and cell metabolites
2. In cell osmotic relations and turgor-related processes
3. In energy transfer reactions
4. In enzyme-catalysed reactions
5. In plant reproduction

However, some other nutrients such as cobalt (Co) and nickel (Ni) were are reported as essential elements in some recent studies. Based on their requirements, plant nutrients are known as macronutrients and micronutrients. Mineral nutrients required for plants in concentration exceeding one part per million (ppm) or 1–150 g per kg of plant dry matter are called macronutrients (C, H, O, N, P, K, Ca, Mg, S), and those required in concentration below 1 ppm are micronutrients or 0.1–100 mg per kg of plant dry matter (Fe, Mn, Cu, Zn, Mo, B and Cl). This classification is arbitrary and has been found to differ with different plant groups and species. It is therefore more appropriate to classify nutrients according to their physiological and biochemical functions. Mengel and Kirkby (2002) have classified plant nutrients into four groups according to their biochemical functions.

Different aspects of nutrient availability, uptake, transport and interactions within nutrients and environmental factors as well as plant responses to their deficiencies and toxicities and their amelioration have been comprehensively reviewed in several publications (Marschner 1995, 2012; Rengel 1999; Mengel and Kirkby 2002; Pandey 2010a). In this chapter the focus is on the main physiological and biochemical roles of nutrients in the plant growth and metabolism.

2.2 Physiological Roles of Macronutrients

2.2.1 Nitrogen

After carbon, hydrogen and oxygen, nitrogen plays a vital role occurring as a major structural constituent of plants. It plays a structural role in combination with carbon, hydrogen, phosphorus and sulphur, as a constituent of varied organic nitrogenous compounds of plants like proteins, nucleotides, porphyrins and alkaloids. Reduction of nitrogen to ammonium (NH_4) is essential for its incorporation into organic compounds to perform various metabolic functions. This involves nitrate reductase which reduces NO_3 to NO_2 and further reduction of NO_2 to NH_4 by nitrite reductase (Campbell 1999). Glutamine and asparagine constitute the main assimilatory amino acids formed by amination of glutamate and aspartate (Temple et al. 1998).

Table 2.1 The nitrogen fractions involved in nitrogen metabolism

Inorganic nitrogen	Low molecular weight organic nitrogen compounds	Macromolecular organic nitrogen compounds
NO_3^- →	Amino acids	Proteins
NH_4^+ →	Peptides	Nucleic acids
N_2 →	Amides	Co-enzymes
	Ureides	Secondary products; membrane constituents
	Amines	

Nitrogen is involved in plant metabolism in inorganic form and two organic forms which maybe LMW (low molecular weight) or HMW compounds (Table 2.1). In green plants, protein N constitutes about 80–85%, nucleic acid N 10% and amino N up to 5% of the total plant N (Kirkby et al. 2009).

To minimize carbon loss, LMW nitrogen-rich compounds such as glutamine, asparagine (amides), arginine (amino acid) and the ureide allantoin are dominant products. They form the major storage and transport forms. These LMW nitrogenous compounds are precursors of amine synthesis and are intermediates for the formation of HMW compounds. Amines form the components of lipid fraction of biomembranes, e.g. ethanolamine. The LMW nitrogen compounds are also involved in osmoregulation in plants. Under saline conditions or water stress, amino acid derivatives proline and glycine betaine counteract the harmful effect of excessive Na^+ and Cl^- and protect enzymes from inactivation (Hasegawa and Bressnan (2000).

The proteins are synthesized from the amino acid. The amino acid involved and the sequence in which they join to produce a polypeptide and proteins is determined genetically. Through the process known as *transcription*, the genome (DNA) produces a template (mRNA) for the synthesis of protein. The order in which the amino acids are arranged in a protein is determined by the nucleotides in the mRNA. The functional properties of a protein are determined by the folding of the polypeptide chains that provides them a three-dimensional structure. This may involve participation of a special group of proteins known as chaperones (Boston et al. 1996).

The proteins function as structural constituents of cell membranes. Many proteins form ligands with metal cofactors to acquire high catalytic efficiency. As intrinsic integrated components of the plasma membranes, the proteins function as ion channels across the membranes. A special class of proteins, known as defence-related proteins, such as *lectins* (Puemans and Van Damme 1995) and *systemins* contribute to plant's defence mechanism against pathogens and mechanical injury (wounding).

Amino acids perform several other functions besides functioning as building blocks of proteins. They may undergo decarboxylation and generate precursors of polyamines, which protect the cellular membranes against toxic effects of superoxide ions, inhibit ethylene biosynthesis and function as signalling molecules. Nicotianamine derived from L-methionine functions as a precursor of phytosiderophores involved in uptake of ferric chelates by strategy II plants and in iron homeostasis (Curie and Briat 2003).

As a constituent of the purine and pyrimidine bases, nitrogen is involved in nucleic acid metabolism. The purine and pyrimidine bases bind to pentose sugars producing nucleosides, which link up through phosphodiester bonds to produce nucleotides that are polymerized to produce the nucleic acids (RNA, DNA). DNA contains two purine (adenine and guanine) and two pyrimidine (cytosine and thiamine) nucleotides (Kirkby et al. 2009). RNA has the same purine components but differs in one of the pyrimidine base (uracil in place of thiamine).

Nitrogen is a structural component of several alkaloids known for their pharmacological properties and also a protective role against tissue damage caused by herbivores. Most alkaloids are synthesized from amino acids – phenylalanine, tyrosine, tryptophan, arginine and lysine.

Several roles have recently been attributed to nitric oxide (NO), produced primarily from L-arginine which is converted to L-citrulline, by NO synthetase. Nitric oxide is an extremely diffusible gas that functions as a signal molecule in response to external and internal factors (Lamattina et al. 2003) and contributes to disease resistance (Delledonne et al. 1998; Grant and Loake 2000) and protection against toxic effects of oxidants. Nitrogen also provides protection to plants which can overcome oxidative stress by maintaining high photosynthesis rates and developing protective mechanisms of the xanthophyll cycle by lower % of the zeaxanthin and antheroxanthin pigments (Huang et al. 2004). The form in which nitrogen is supplied has also been reported to affect the damage to plants. Thus plants grown with nitrate show more tolerance to photodamage than plants grown with ammonium as observed by Zhu et al. (2000) in bean plants. The plants grown with ammonium showed higher levels of lipid peroxidation. Nitrogen affects the biosynthesis of phenolic compounds and thus alters the oxidative status of the cell (Sanchez et al. 2000; Kovacik and Klejdus 2014). Variations were observed in the antioxidant system in nitrogen-deficient plants which was also mediated by NO signalling (Kovacik et al. 2009, 2014). Medina-Pérez et al. (2015) showed that the phenylpropanoid biosynthesis as well as the antioxidant status increased, to overcome the oxidative stress under nitrogen deficiency (Virginia et al. 2015). Kausar et al. (2017) recently observed that nitrogen could provide protection against oxidative damage by enhancing the antioxidant defence system.

2.2.2 *Phosphorus*

The uptake of phosphorus is active and does not involve reduction, and it remains in its oxidized state within the cell. It is taken up primarily as $H_2PO_4^-$, and it occurs either as its inorganic form (Pi) or as organophosphorus compounds (Raghothama 1999). Phosphate is bound in a diester linkage (C-P-C) to form essential compounds of biological membranes. Its esterification to carbon unit by a hydroxyl group (C-O-P) forms an organic phosphate ester (e.g. sugar phosphate), or it may be attached to form the energy-rich pyrophosphate bond P~P, e.g. ATP. Another organic P compound is phytin, a storage form which occurs as Ca and Mg salts of phytic acid formed during seed formation (Bielski 1973).

The structural role of phosphorus is as a constituent of biomembranes and nucleotides. It is a major component of the lipids of the plant membranes occurring as phospholipids, e.g. phosphatidylcholine. The phospholipids form the central hydrophobic barriers of the cell membrane, and the ease with which they move freely in the plane of the membrane and undergo reorientation within the lipid bilayer accounts for the fluidity of the membranes. Gniazdowska et al. (1999) reported that a low phospholipid concentration and modification of relative composition of membrane would accentuate lipid peroxidation. Kandlbinder et al. (2004) reported the increase in H_2O_2 in phosphorus-deficient bean roots due to triggered redox changes resulting in oxidative stress. Juszczuk et al. (2001) showed that the roots deficient in phosphorus showed accumulation of phenolics and enhanced activities of other scavenging enzymes such as POD (peroxidase), CAT (catalase) and SOD (superoxide dismutase). Recently Hernandez and Munne-Bosch (2015) have shown that phosphorus deficiency can alter the photosynthetic apparatus, reduce CO_2 assimilation rates, downregulate genes for photosynthesis and ultimately produce photoinhibition at the photosystem II level, which result in photooxidative damage.

Structurally phosphorus is also involved in linking up of nucleosides to produce nucleotides that polymerize to produce long chains of nucleic acid DNA molecules which are carriers of genetic information and RNA which is responsible for translocation of genetic information. The phosphate groups join the 5′ carbon of one nucleoside to 3′ carbon of the next nucleoside by a covalent phosphodiester bond. The directional nature of these bonds accounts for two distinct ends (5′ or 3′) of the nucleic acids. The phosphate linking of the nucleosides accounts for the acidic nature of nucleic acids and also for high phosphorus content in the nucleic acid-rich meristematic regions of plants (Berg et al. 2015).

Phosphorylated compounds that contain pyrophosphate bonds (℗~℗) function as an energy-conserving mechanism. The most important compound is adenosine triphosphate (ATP) through which energy is supplied for endergonic process such as active uptake and biosynthesis of compounds by transfer of phosphoryl group. The pyrophosphate bond of adenine triphosphates can be transferred to other nucleoside phosphates (UDP-℗; GDP~℗). Hydrolysis of pyrophosphate bond yields energy that activates enzymes and drives reactions which are otherwise energetically unfavourable. Energy released by hydrolysis of pyrophosphates by proton pumping phosphorylases located in the tonoplast drives the proton pump leading to acidification of the vacuole and generation of electrochemical gradients driving membrane transport (Palmgren 2001). Phosphorylation of enzyme proteins by protein kinases plays an important role in regulation of enzyme like nitrate and phosphoenolpyruvate carboxylase.

The role of phosphorus in energy transduction also stems from its role as a structural constituent of the coenzymes NAD, NADP, FAD and FMN, which function as redox agents during mitochondrial electron transport. Thiamine pyrophosphate, with a high-energy group transfer potential, plays a key role in carbohydrate metabolism. Coenzyme A is involved in fat, protein and carbohydrate metabolism. Several phosphorus-containing compounds such as inositol 1, 4, 5-triphosphate, cAMP, cGMP and phosphatidic acid function as second messengers or signalling molecules (Zhang et al. 2003). They have also been shown to be involved in phospholipase C inactivation and opening and closing of transmembrane channels for K^+, Na^+ and Ca^{2+}.

Phosphate esters play an important role in cellular metabolism and photosynthetic pathways (Grossman and Takahashi 2001; Maathuis 2009). As many as 50 sugar phosphates are known from plants. Plants have two major phosphate pools; each maintains an equilibrium in concentrations of its constituents through enzyme-catalysed reactions (Fujita et al. 2004). One of these pools, the *hexose phosphate pool*, is made up of three intermediates of the glycolytic pathway – glu-6-phosphate, glu-1-phosphate and fruc-6-phosphate – maintained in equilibrium by phosphoglucomutase and glucose-6-phosphate isomerase. This pool provides the precursor for synthesis of sucrose and starch. The other pool – the *triosephosphate/pentose phosphate metabolic pool* – is made up of several sugar phosphates maintained in equilibrium through enzyme-catalysed interconversions. This pool contributes to the energy-conserving reactions (ATP synthesis) during the later phase of glycolysis and also for the nucleic acid synthesis. It also provides the precursors of the initial reactions of the shikimate pathway (Rychter and Rao 2005).

Fairly large quantities of phosphorus may be stored in seeds in the form of a cation salt of *myo*-inositol hexaphosphoric acid, or *phytate*. The function of phytate is evident during seed germination where it provides the large requirement for nutrients. Phytates form a major pool for the storage of K, Mg and Ca. Phytic acid has a high affinity for heavy metals, to which it binds, reducing their free concentration in the cytoplasm. This contributes to tolerance of hyperaccumulator plants to excess concentrations of heavy metals (Van Steveninck et al. 1993). Binding of heavy metals to phytic acid also contributes to bioextraction and phytoremediation of heavy metal toxicities (Bolan et al. 2003).

Vacuolar Pi is the non-metabolic pool and serves as a reserve supplying cytoplasm with phosphate when necessary. The regulation of metabolic pathways in the cytoplasm and chloroplasts is to a large extent controlled by compartmentation of Pi. Many key enzymes are controlled by Pi. The activity of ADP-glucose phosphorylase is inhibited by Pi and results in poor starch synthesis. Carbon fixation is also inhibited by high Pi concentration. The efficiency of translocation of Pi and its utilization is involved in N_2 fixation and photosynthesis in plants (Tak et al. 2012). The sink activity of stem is affected by P deficiency, which suppresses photosynthetic translocation, causes accumulation of carbohydrate in the source leaves and ultimately results in depression of photosynthesis (Fujita et al. 2004; Chaudhary et al. 2008). Phosphorus also plays an important role in gene expression and signal transduction (Fang et al. 2009).

2.2.3 Potassium

Potassium is taken up at a very high rate by the plants due to the high permeability of plant membranes to K^+. It is characterized by a high mobility in entire plant, and it is translocated towards younger tissue (Wang and Wu 2013). A closely knit regulation between the water channels and the potassium uptake channels helps to maintain plant homeostasis (Liu et al. 2006). It is abundant in cytoplasm and helps in neutralizing insoluble macromolecular anions to maintain ionic balance and osmoregulation in plant cell (Kanai et al. 2011). Its large accumulation in cell vacuoles contributes to turgor-driven extension growth of cells. Deficiency of potassium leads to decrease in turgor and cell size which is reflected in decrease in leaf area and stem elongation (White and Karley 2010). Inadequate supply of potassium restricts meristematic growth and cambial activity. Potassium is beneficial for cambial growth and wood formation, and this is related to potassium involvement in osmoregulation in the expanding cambial cells (Wind et al. 2004). Potassium plays a role in opening and closing of stomata (Talbot and Zeiger 1996; Hosy et al. 2003; González Benlloch et al. 2008). Activation of membrane-bound proton pumping ATPases causes increased uptake of K^+ (Wu and Assmann 1995), which increases the osmotic pressure, causing water uptake from the adjoining cells. This increases the turgor and leads to opening of stomata. Reversal of this process during darkness tends to close the stomata.

In cytosol and chloroplasts, where potassium concentrations are sufficiently high (100–200 μM), potassium neutralizes the anionic charges (NH_3^-, Cl^-, SO_4^-). It also forms electrostatic bonds with the carboxylic groups of organic acids produced during cellular metabolism. Neutralization of acid groups by potassium leads to stabilization of cytosolic and chloroplastic pH to a slightly alkaline reaction (pH 7–8), which is favoured for optimal activation of most enzymes localized in cytoplasm or chloroplasts. Low rates of CO_2 fixation in potassium-deficient plants are attributed to its role in stabilizing the pH of the stroma to a level that is optimum for the activity of the Calvin cycle enzymes. Potassium thus affects the photosynthesis in plants (Zhao et al. 2001; Wang et al. 2012).

Potassium activates about 50 enzymes by producing conformational changes in enzyme protein (Mengel 2001). Potassium is an activator of formate-formyltetrahydrofolate synthetase and succinyl-CoA synthetase. Together with Mg^{2+}, it activates acetic thiokinase, pyruvate kinase and glutathione synthetase. It has been suggested that potassium activation of enzymes involves a change in conformation of the enzyme protein which augments the rates of catalysis and in some cases the affinities of the enzymes for the substrates. Low activities of certain enzymes such as Rubisco in potassium-deficient plants have been attributed to potassium effect on protein synthesis, which is due to a role of potassium in binding of tRNA to the ribosomes (Wyn-Jones et al. 1979).

Potassium also plays an important role in providing tolerance to plants exposed to various biotic and abiotic stresses including pathogen, water deficit and water logging and osmotic and temperature stressing (Shabala and Cuin 2008; Devi et al. 2012; Wang et al. 2013). Potassium effect on cells turgor also accounts for its role in light-driven movements. In cereals, potassium is known to contribute to mechanical strength of the straw that provides protection against lodging. Potassium also improves resistance of plants against pathogenic fungi, nematodes and other microorganisms (Prabhu et al. 2007).

Cakmak (2005) observed that potassium provides protection to plants from high intensity of light as plants grown under prolonged conditions of high light have a greater requirement of potassium for normal growth. They suggested that stomatal closure due to potassium deficiency leads to photoinhibition and poor photosynthetic CO_2 fixation (Cakmak and Engels 1999). Disturbances in photosynthetic CO_2 fixation lead to activation of molecular O_2 to produce ROS which degrade chlorophyll and membranes and make the deficient plants more susceptible to damage by high light intensity (Zhao et al. 2001).

Another factor involved in production of ROS is increased rates of NADPH oxidase which accelerates production of $O_2^{\bullet-}$ in potassium-deficient plants (Cakmak 2005). High potassium in plants can decrease ROS by decreasing NADPH oxidase activity. Cakmak (2005) also reported that potassium deficiency enhanced activity of enzymes like ascorbate peroxidase and guaiacol peroxidase to detoxify H_2O_2. Since ROS production is reduced by potassium, it is suggested that supplying potassium to plants would help them to overcome environmental stress conditions (Marschner and Cakmak 1989).

The role of ROS in potassium uptake by roots has also been reported. Shin and Schachtman (2004) showed that K^+ uptake kinetics is governed by ROS produced in the roots due to potassium deficiency by modulating the gene expression and physiological changes. They observed that ROS accumulated in regions of roots that were high in K^+ uptake and translocation. The up-regulation of genes due to deficiency of potassium was also prevented by decrease in NADPH oxidase (which produces ROS) in *Arabidopsis* (*rhd2*). Shin et al. (2005) determined the role of ROS in wild-type *Arabidopsis* and different root hair mutants under nitrogen, phosphorus and potassium deficiency. They observed that changes in ROS concentrations in hair cells in case of nitrogen and potassium deficiency and in cortical cells in phosphorus-deficient plants played an important role.

Kim et al. (2010) isolated a member of family of peroxidases, RCI3 (for Rare Cold Inducible gene 3). They observed overexpression of *RCI3 (RCI3-ox)* resulted in ROS production and *AtHAK5* expression in potassium deficiency indicating low-potassium signal transduction pathway in roots of *Arabidopsis*. Previously, it was observed by Shin and Schachtman (2004) and Jung et al. (2009) that expression of *AtHAK5* is related to production of ROS. Both the reports suggest that under potassium deficiency, ROS production due to RCI3 increased expression of *AtHAK5*. Hafsi et al. (2014) reported that activation of signalling cascades such as ROS, phytohormones (ethylene, auxin and jasmonic acid), Ca^{2+} and phosphatidic acid helped in overcoming potassium deficiency.

2.2.4 Sulphur

Sulphur is taken up by plants mainly from soil in form of sulphate (SO_4^{2-}) and is subsequently assimilated into several organic compounds (Droux 2004; Anjum et al. 2015). Conversion to organic sulphur compounds may take place both as

SO_4^{2-} and after its reduction to sulphide (S_2^{2-}). The reduced and oxidized forms are easily interconvertible ($SO_4^{2-} \leftrightarrow S_2^{2-}$). Sulphate is directly incorporated into sulpholipids, polysaccharides, glucosinolates and certain phytoalexins (Leustek et al. 2000; Sanda et al. 2001; Mikkelsen et al. 2002). Reduction of sulphide leads to its incorporation into many other compounds such as the amino acids cysteine and methionine, coenzymes and secondary metabolites. Both cysteine and methionine are important constituents of plant proteins. These amino acids acquire added significance because animals and humans lack the ability to reduce sulphur and depend on plants for meeting their dietary requirements. Decrease of storage proteins – albumin, globulins, glutelins and prolamins – especially globulins, has been reported in response to sulphur deficiency in soya bean seeds (Chandra and Pandey 2016). Since cysteine is a major constituent of globulin, the decrease in globulins could be due to poor cysteine levels because of sulphur deficiency (Shewry et al. 1995).

The cysteine residues of proteins are critical for their structure and function. The tertiary structure of proteins is determined by the oxidation of the thiol (SH) group of cysteine to produce covalent disulphide bond (S-S). Interconversion of thiol and disulphide bonds also provides a mechanism for regulation of enzyme activities. Cysteine functions as a precursor of some low molecular weight peptides of high biological activity. Important amongst these are glutathione and thioredoxins. Glutathione is a tripeptide formed from glutamine, cysteine and glycine. Predominantly present in the reduced form (GSH), it can be readily converted to its oxidized form (GSSG), a property which enables it to function as a buffer of cell's redox potential. Enzymatic interconversion of GSH and GSSG provides an efficient mechanism for regeneration of ascorbate oxidized to dehydroascorbate by ascorbate peroxidase as a part of cell antioxidant mechanism (Noctor and Foyer 1998). Glutathione also offers protection to plants against toxic effects of xenobiotics (Gill et al. 2013).

Sulphur offers protection against toxic accumulation of heavy metals by phytochelatins. Plants subjected to excess concentrations of heavy metals show induction of phytochelatin synthase, which catalyses the synthesis of the low molecular weight polypeptides known as *phytochelatins* from glutathione (Rauser 1995). Metallothioneins are a group of polypeptides rich in cysteine and are formed in response to heavy metal toxicity (Cd, Zn). Phytochelatins and thioneins provide a mechanism for their detoxification by binding of the free heavy metal cations to their thiol groups (Cobbett and Goldsbrough 2002).

The sulphur thioredoxins and the associated enzyme thioredoxin reductase are important for regulation of enzyme activities. Thioredoxin reductase from chloroplasts is ferredoxin dependent (Schrümann and Jacquot 2000). The thioredoxin-thioredoxin reductase system activates several enzymes, e.g. fructose 1,6-phosphate, by catalysing reduction of their disulphide bonds. Thioredoxin-mediated thiol-disulphide reduction is also involved in the activity of *peroxiredoxins*, which not only catalyse peroxidation reactions but also play a role in antioxidant defence mechanism and modulation of redox signalling during development (Lee et al. 2005; Kapoor et al. 2015).

Sulphur binds to iron to produce iron-sulphur clusters (Fe-S) that form integral part of several iron proteins. The low molecular weight (9 kD) electron-carrier protein ferredoxin that is widely and abundantly present in plants plays a major role as a donor or acceptor of electrons in plant metabolism (Gerber and Lill 2002. It is largely localized in chloroplasts and root plastids (Takahashi et al. 2011).

Sulphur, in reduced form, is also a constituent of many vitamins and coenzymes – biotin, coenzyme A and thiamine pyrophosphate. Biotin functions as a mobile carbonyl group carrier in a variety of enzyme-catalysed carboxylation (Alban et al. 2000) reactions involved in lipid biosynthesis, leucine catabolism and isoprenoid metabolism. Secondary metabolites such as glucosinolates, stored in plant vacuoles of Brassicaceae and several other dicotyledonous families, and of allin, present in *Allium* sp. are also sulphur compounds.

Polysulphides play an important role in managing the thiols in order to maintain a balance in the redox status of the cell and prevent cell death (Jacob and Anwar 2008). The thiol/polysulphide redox reactions produce the reductant perthiol (RSSH) which in turn easily produces $O_2^{\bullet -}$ (Munday et al. 2003). After reducing O_2 to $O_2^{\bullet -}$, the RSSH is oxidized to $RSS^{\bullet}$ (perthiyl radical). The latter dimerizes to form RSSSSR (polysulphide) or it reacts with GSH to form $RSSSG^{\cdot -}$ (polysulphide anion). The GSH detoxify ROS to generate GSSG, which can be reduced back to GSH, by the NADPH-dependent enzyme glutathione reductase (Lillig et al. 2003).

Kandlbinder et al. (2004) observed that sulphur deficiency resulted in redox changes which induce oxidative stress. Under stress conditions, increase in ROS enhances the glutathione accumulation (Willekens et al. 1997; Gill et al. 2013). The enhanced glutathione accumulation due to H_2O_2 generation was shown to affect the sulphur uptake rate in the barley leaves (Smith et al. 1985). Contrary to other reports, Lappartient and Touraine (1997) observed decrease in GSH in roots exposed to H_2O_2. Probably feedback inhibition of γ-ECS by GSH controls the overall GSH synthesized (Smith et al. 1985). In sulphur-deprived rice, the concentration of GSH was severely reduced (Lunde et al. 2008). A decrease in the concentration of non-protein thiols and increase in SOD, CAT, POD, APX (ascorbate peroxidase) and GR observed in sulphur-deficient wheat and black gram were observed by Chandra and Pandey (2014a, b).

2.2.5 Calcium

Calcium is present in plant tissue as Ca^{2+}, or as Ca carbonate, Ca phosphate and Ca oxalate. The uptake of Ca^{2+} is very slow as it is absorbed only by young root tips. The uptake is a passive process and is competitively depressed by presence of K^+ and NH_4^+. A low level of calcium is maintained in the cytoplasm to prevent unfavourable interactions with other nutrient ions (PO_4^-, Mg^{2+}) and inactivation of enzymes. It is also a prerequisite for its functioning as a second messenger. Low concentration of calcium in cytoplasm (~0.2 μM) is maintained by regulation of Ca^{2+} fluxes across the cellular and subcellular membranes (Evans et al. 1991) involving membrane transporters (Ca^{2+}-ATPase). Efflux of Ca^{2+} from cytosol into the vacuole involving V-Ca^{2+}-ATPase activity builds up high concentration of Ca^{2+} in vacuoles, where it plays a role in neutralization of anions and in osmoregulation. Osmoregulation of cells is controlled by the Ca oxalate in the vacuoles. Calcium thus plays an electrochemical role by functioning as neutralizing ion for anions. Pumped into the vacuole by the membrane transporter (V-Ca^{2+}-ATPase), calcium neutralizes the anions – phosphate, citrate, malate and/or oxalate – that may get accumulated in vacuoles in high concentrations (Marschner 2012).

Calcium functions as a structural constituent of cell walls because a high concentration is found in the cell wall (apoplasm) in middle lamella region and exterior surface of plasma membrane. The carboxylate ions ($RCOO^-$) of polygalacturonic acid (pectin) are bound to the calcium in the middle lamella, and thus it performs the most essential function of regulating membrane permeability and strengthening the cell walls (White and Broadley 2003). Calcium deficiency inhibits the growth of middle lamella during the cell expansion. Calcium pectate provides strength to the cell wall as it makes the tissue resistant to degradation by polygalacturonase. Ability of calcium to act as a bridge between phosphates and carboxyl groups of phospholipids and proteins accounts for its role in providing stability to cellular membranes. In calcium-deprived plants, the membrane structure disintegrates, there is poor compartmentation of Ca^{2+}, and low molecular weight solutes exhibit leakage. Therefore calcium deficiency results in impairment of membrane permeability and their disintegration. High calcium content in fruits therefore increases firmness of fruit. During ripening intracellular redistribution of Ca^{2+} results from increased activity of polygalacturonase so that the ethylene-generating system is activated, thus enhancing fruit ripening. Along with phytohormones, Ca^{2+} is also involved in regulation of senescence (Ali et al. 2007).

Calcium plays an important role in cell extension. Root growth is inhibited by calcium deficiency. Pollen tube growth and direction of pollen tube are controlled by extracellular calcium gradient. Calcium is present in very small amounts in cytoplasm, and this is important as calcium inhibits enzymes located in cytoplasm and chloroplast, e.g. PEP carboxylase and hexodiphosphatase. Calcium increases activity of certain enzyme like α-amylase, phospholipase and ATPases. Activation of α-amylase in aleurone layers by gibberellic acid and its inhibition by abscisic acid are attributed to their effect on transport of calcium to endoplasmic reticulum, which forms the site for the synthesis of the enzyme. Mitochondrial enzymes may be activated by calcium, e.g. glutamate dehydrogenase. Calcium plays a regulatory role by activating biochemical events in response to environmental stresses, mechanical stimuli and pathogen infections (Bush 1996; Knight 2000).

A recent role assigned to calcium is that of a second messenger (Hetherington and Brownlee 2004; Heplar 2005). Perception of stress signals causes transient opening of calcium channels and pumping of calcium into the cytoplasm causing increase in its cytosolic concentration. This activates calcium-binding proteins such as calmodulin. Calmodulin is a polypeptide which binds four Ca^{2+}, forming a compact structure. Calmodulins are also involved in synthesis of actin filaments, cell division cycle and pollen-stigma interaction in plants. Binding of Ca^{2+} to calmodulin changes its tertiary structure exposing a patch of methionine, leucine and phenylalanine involved in binding of calmodulin to the target proteins and their activation. Calmodulin is involved in most stress responses as well as phospholipid signalling (Zielinski 1998; Saijo et al. 2000; Snedden and Fromm 2001; Reddy et al. 2002). It regulates the levels of free calcium in cytosol and enzyme activation (Romeis et al. 2000). Calmodulin is known to activate several higher plant enzymes like cyclic nucleotide phosphodiesterase, adenylate cyclase, NAD kinase including Ca^{2+} ATPases and protein kinases involved in cell signalling (Tuteja and Mahaja 2007). A pistil-expressed Ca^{2+}-binding protein (PCP) in anther and pistil is suggested to be involved in pollen-pistil interaction (Furuyama and Dzelzkalns 1991). Calcium-dependent protein kinases (CDPKs) are also implicated in pollen development (Saijo et al. 2000).

A very significant role has been assigned to the calcium signalling in plants produced in response to a wide array of unfavourable environmental conditions (Ng and McAinsh 2003; White and Broadley 2003; Ma and Berkowitz 2011). Yang and Poovaiah (2002) reported that the calcium in the cytoplasm can enhance NADPH oxidase resulting in ROS production. According to them, abiotic stress can trigger an influx of calcium in the cytosol and stimulate H_2O_2 production. They suggested that cytosolic calcium has a dual role in regulating H_2O_2 homeostasis. It can either reduce H_2O_2 levels by stimulating the catalase activity via the Ca^{2+}/CaM or generate H_2O_2 by directly activating NADPH oxidase.

2.2.6 Magnesium

Even though abundant in soil solution, magnesium (Mg^{2+}) is taken up by plant concentrations much lower than the other cationic macronutrients (Wanli et al. 2016). This is possibly because of strong cation competition in uptake and lack of magnesium transporters in plasmalemma. The uptake of Mg^{2+} is depressed by low pH and cations like K^+, NH_4^+, Ca^{2+} and Mn^{2+}. The uptake rate is very slow and passive. Magnesium performs very diverse functions. The function of magnesium is related to its mobility within cells. The major function of magnesium stems from its being a central atom of chlorophyll molecule. A central magnesium atom is coordinated to the nitrogen atoms of the four modified pyrrole rings forming a porphyrin-like structure. Chlorophyll magnesium may constitute 10% or more of the total leaf magnesium. The total protein (almost 25%) in leaf cells is localized in chloroplasts, and therefore magnesium deficiency results in poor chlorophyll content, small size of the chloroplasts and reduction in electron transfer in photosystem II. Magnesium also helps to maintain the structural integrity of ribosomes and binding of the ribosomal aggregates to tRNA, a process necessary for protein synthesis (Maathuis 2009).

Only a relatively small proportion of total plant Mg^{2+} (20%) is required for various function in chloroplasts and cytoplasm. The rest of Mg^{2+} occurs as counterions for organic acid anions and inorganic anions in the vacuole and for pectates in the middle lamella of cell walls. Like potassium, magnesium is also important in maintenance of ionic balance and stabilization of pH. Vacuolar concentration of magnesium is particularly important for osmoregulation and turgor-driven cell growth (Shaul 2002). Starch is accumulated, and rate of photosynthesis and respiration is low under magnesium deficiency.

Magnesium is an activator of several enzymes. Some of these are activated by Mg^{2+} along with another cation (usually K^+). In most cases, activation by magnesium is not specific and can be achieved, to varying extents, by other cations, mostly Mn^{2+}. Most magnesium-activated enzymes catalyse transfer of a phosphate group or a carboxyl group. Magnesium functions in enzyme activation in two ways. In some enzymes, it functions as a freely dissociable cofactor. In others, it binds to the substrate modifying it to a form that is more favourable to enzyme-substrate interaction (Clarkson and Hanson 1980). ATPases, phosphorylases and phosphokinases belong to the second category. Mg^{2+}-ATP, and not free ATP, forms the substrate for ATPases (Cowan 2002). High concentration of Mg^{2+} is required in chloroplasts and cytoplasm for maintaining a high pH. The high pH is required to form the Mg-ATP complex necessary for energy-rich phosphoryl group transfer by the ATPases. The Mg^{2+} forms a bridging component between ADP for synthesis of ATP. In plants that are adequately fed with magnesium, essentially all nucleoside triphosphates occur in the form of their magnesium complexes. The enzyme fructose-1,6-diphosphatase and RuBP carboxylase require Mg^{2+} and high pH for optimum activity. Key enzyme glutamate synthetase has magnesium requirement. Magnesium is essential for RNA polymerase and hence synthesis of RNA. Deficiency of magnesium therefore depresses protein synthesis (Marschner 2012).

A major role of magnesium involves phloem loading and unloading of sucrose. Magnesium-deficient plants show increased accumulation of sugars in the leaves and a high ratio of shoot/root dry weight (Cakmak et al. 1994a, b; Hermans and Verbruggen 2005). This results in poor export of phloem photoassimilates from Mg-deficient leaves (Cakmak and Kirkby 2008; Cakmak 2013). Low starch content of cereal seeds and potato tubers also reflect impaired source-sink relationship. Restricted loading of phloem is attributed to low activity of proton pumping ATPases (proton-sucrose cotransport) which require magnesium for activation. High concentration of sugars in source leaves of magnesium-deficient plants caused by restricted loading of phloem may cause feedback inhibition of carboxylase activity of Rubisco and a shift in favour of its oxygenase activity. This pattern of high sugar level and shoot/root ratio in magnesium-deficient plants is also similar to that in potassium-deficient plants, but this is in contrast to the low shoot/root ratio and low levels of sugar in nitrogen- and phosphorus-deficient plants (Cakmak et al. 1994a; Freeden et al. 1990; Rufty et al. 1988; Marschner et al. 1996; Hermans et al. 2006) indicating that the latter deficiencies have less effect on root growth (Cakmak 2005; Hermans et al. 2005; Marschner 1995, 1996). Potassium- and magnesium-deficient plants are also highly light sensitive exhibiting leaf chlorosis (Marschner and Cakmak 1989; Cakmak 2005) which is not observed in phosphorus deficient plants (Cakmak 1994). Cakmak (1994) and Marschner and Cakmak (1989) correlate this to higher sugar accumulation in Mg- and K-deficient plants.

Severe magnesium deficiency decreases photosynthetic electron transport in the PSII and PSI as observed in pine (Laing et al. 2000) and sugar beet plants (Hermans et al. 2004). This leads to activation of molecular oxygen (O_2) and production of ROS, exposing the magnesium-deficient plants to oxidative damage, which acquires serious proportions under high intensity of light or photoinhibitory conditions (Marschner and Cakmak 1989). Magnesium deficiency thus enhances the antioxidative enzymes like APX and GR (Cakmak and Marschner 1992a, b). Activation of antioxidative defence systems due to magnesium deficiency has been reported in *Mentha* by Candan and Tarhan (2003) and in pepper by Riga et al. (2005). Oxidative damage as evident by increase in malondialdehyde (MDA), H_2O_2 and antioxidative enzymes like SOD, CAT, APX and GR was also observed by Esfandiari et al. (2010).

2.3 Physiological Roles of Micronutrients

2.3.1 Iron

Iron is a transitional metal that exists as ferrous (Fe^{2+}) and ferric (Fe^{3+}) ions. The easy conversion of the two forms ($Fe^{2+} \leftrightarrows Fe^{3+}$) accounts for its role in a variety of redox reactions (Briat et al. 2007; Rout and Sahoo 2015). Iron has high affinity for oxygen and forms stable complexes with organic ligands. It acquires high biological activity by binding to proteins. Iron proteins function as enzymes catalysing redox reactions and as electron carriers in photosynthetic and mitochondrial electron transport systems. Iron is bound to the apoprotein in four forms:

(a) It forms ionic bonds with the protein amino acids, e.g. superoxide dismutase (Fe-SOD). Bonds are also formed between two coupled iron atoms and a protein (Berthold and Stenmark 2003), e.g. alternative oxidase.
(b) Iron ions form coordination bonds with sulphide ions and bind to the apoprotein in the form of iron-sulphur clusters (Fe-S, 2Fe-2S, 4Fe-4S) as ferredoxin.
(c) Iron-sulphur cluster along with a flavin nucleotide (FMN or FAD) forms the cofactor, e.g. succinic dehydrogenase.
(d) Iron ion is chelated to nitrogen of the four pyrrole groups of porphyrin IX to form a heme prosthetic group, e.g. catalases, peroxidases and cytochrome c oxidase.

Iron is a cofactor of many dioxygenases (Presscott and John 1996) and monooxygenases (Chapple 1998), which catalyse the incorporation of oxygen (O_2) directly into the substrates. Iron dioxygenases are best exemplified by lipoxygenases involved in the hydroperoxy fatty acids, and production of oxylipins, derivatives of which function as signalling molecules (Feussner and Wasternack 2002). Some iron-containing dioxygenases require an additional substrate, generally 2-oxoglutarate. Several iron-containing gibberellin oxidases belong to this category. The iron enzyme 1-aminocyclopropane-1-carboxylic acid oxidase is an ascorbate-dependent dioxygenase responsible for synthesis of ethylene. There is involvement of several

P_{450} monooxygenases in synthesis of gibberellins and jasmonic acid. Many genes encoding for the cytochrome P_{450} monooxygenases (the CYP gene family) have been cloned and characterized (Chapple 1998).

Iron enzymes and electron-carrier proteins are essential constituents of mitochondrial and photosynthetic electron transport. Mitochondrial electron transport involves transfer of electrons from NADH and $FADH_2$, produced during the citric acid cycle, to molecular oxygen through the electron-carrier proteins localized in the mitochondrial membrane which contain iron as an integral constituent. Transport of electrons through the electron-carrier proteins generate a proton gradient required for the ATP synthesis (oxidative phosphorylation). Iron is essential for harvesting of solar energy and transport of electrons resulting from splitting of water (H_2O) through photosystem II and photosystem I. It is a constituent of the PSII reaction centre and that of ferredoxin, the terminal recipient of the electrons from PSI. In the former iron occurs in the ionic form and in the latter in the form of iron-sulphur (4Fe-4S) cluster. Transport of electrons from PSII to PSI is linked through the heme protein complex cytochrome *bf* and the copper protein plastocyanin.

Being a cofactor of the enzymes, iron is also involved in nitrogen metabolism. Nitrate reductase and nitrite reductase are two iron enzymes involved in reduction of nitrate to ammonium. Nitrate reductase has three domains – heme, molybdopterin and flavin. Nitrite reductase is a 4Fe-4S siroheme. Glutamate synthase (GOGAT), which converts glutamine to glutamate, also requires iron for catalysis. In legumes iron also acts as a cofactor of dinitrogenase and dinitrogen reductase in fixation of atmospheric nitrogen. The inactivation of nitrogenase is prevented by iron protein leghemoglobin, which has higher affinity for O_2. Iron fertilization of nodulating legumes benefits both dry matter production and nitrogen contents (Tang et al. 1990). Some important iron enzymes of higher plants and reactions catalysed by them are listed in Table 2.2. As an important constituent of the photosynthetic and mitochondrial ETC, iron deficiency disrupts the ETC and results in ROS production. The Fe^{3+}/Fe^{2+} redox potential imparts a dual role to iron in free radical chemistry. Thus it functions as a prooxidant by generating the highly toxic $OH^{\cdot}$ radical on one hand, and at the same time, it acts as an antioxidant by being a constituent of several antioxidant enzymes (Sharma 2006). Toxic concentrations of iron also initiate oxidative damage through Haber-Weiss reaction which produces the overtly toxic $^{\cdot}OH$ radical:

$$H_2O_{+}O_2^{\cdot -} \rightarrow O_2 + HO^{\cdot} + HO^{-}$$

It is an iron-catalysed reaction and proceeds via the following steps:

$$Fe^{3+} + O_2^{\cdot -} \rightarrow Fe^{2+} + O_2$$

$$Fe^{2+} + H_2O_2 \rightarrow Fe^{3+} + HO^{\cdot} + HO^{-}$$

$$O_2^{\cdot -} + H_2O_2 \rightarrow O_2 + HO^{\cdot} + HO^{-}$$

Table 2.2 Some important iron enzymes in plants

Enzyme	Reaction catalysed
Superoxide dismutase (Fe-SOD)	$2O_2^{\cdot -} + 2H^+ \longrightarrow H_2O_2 + O_2$
Alternative oxidase	Ubiquinol + $O_2 \longrightarrow$ ubiquinone + H_2O
Lipoxygenase	Linoleic acid $\longrightarrow$ 13 or 9 hydroperoxylinoleic acid
Aconitate hydratase	Citrate $\longrightarrow$ isocitrate
Nitrite reductase	$NO_2^- + 6Fdx_{(red)} + 8H^+ \longrightarrow NH_4^+ + 6Fdx_{(ox)} + 2H_2O$
Sulphite reductase	$SO_3^{2-} + 6Fdx_{(red)} \longrightarrow S_2^- + 6Fdx_{(ox)}$
Glutamate synthase	Glutamine + 2 oxoglutarate + $2Fdx_{(red)}$ or NADH $\longrightarrow$ glutamate + $2Fdx_{(ox)}$ or NAD^+
Succinate dehydrogenase	Succinate + FAD $\longrightarrow$ fumarate + $FADH_2$
NADH – Q oxidoreductase	$NADH + UQ + 5H^+_{(matrix)} \longrightarrow NAD^+ + UQH_2 + 5H^+_{(Cytsol)}$
Succinate – Q oxidoreductase	Succinate $\xrightarrow{e}$ FAD $\xrightarrow{e}$ UQ $\xrightarrow{e}$ UQH_2
Fdx – $NADP^+$ oxidoreductase	$2Fdx_{(red)} + NADP^+ \longleftrightarrow 2Fdx_{(ox)} + NADPH + H^+$
Catalase	$H_2O_2 + H_2O_2 \longrightarrow 2H_2O + O_2$
Peroxidases	$H_2O_2 + AH2 \longrightarrow 2H_2O + A$
Cytochrome c oxidase	$O_2 + 4H^+ + 4e^- \longrightarrow 2H_2O$
Cytochrome c reductase	$QH_2 + 2Cyt\ c_{(ox)} + 2H^+ \longrightarrow Q + 2Cyt\ c_{(red)} + 4H^+$

Fe^{2+} may also react with molecular oxygen (O_2) to produce still more toxic compounds such as ferryl ($Fe^{2+}O$) or perferryl ($Fe^{2+}O_2$). These highly reactive oxygen species cause damage to membrane lipids, proteins and DNA and induce mutations. Free radical reactions are initiated by toxic iron by binding to proteins, phospholipids and DNA. Another way iron could contribute to production of ROS is through action of lipoxygenase. This iron enzyme may also catalyse the production of $^1O_2$.

While free ionic iron enhances the generation of ROS (Becana et al. 1998; Halliwell and Gutteridge 2007), iron proteins contribute to their effective detoxification as an important constituent of heme enzymes (CAT, POD and APX) or non-heme enzymes Fe-SOD. The oxidative stress may be induced by iron deficiency due to decrease in antioxidant enzymes like SOD, CAT and POD which have iron as a constituent. Iron deficiency may affect both the generation of reactive species and the antioxidative defences (Iturbe-Ormaetxe et al. 1995; Becana et al. 1998). The iron isoenzymes of superoxide dismutase (Fe-SOD) carry out the detoxification of $O_2^{\cdot -}$ by dismutating them to H_2O_2. Kurepa et al. (1997) observed that both the *SodB* transcripts and Fe-SOD enzymes decreased in Fe-deficient *Nicotiana tabacum*. Another iron enzyme, alternative oxidase (AOX) of the mitochondrial ETC provides an alternate pathway to the reducing equivalents from quinol and prevents them from interacting with oxygen to generate ROS (Purvis 1997; Millenaar et al. 1996). The heme enzymes CAT, POD and APX are important for H_2O_2 detoxification in plants, and their activities are affected by iron deficiency (Raineri et al. 2001; Shigeoka et al. 2002; Sun et al. 2007). Iron deficiency of plants is reported to cause oxidative damage and results in marked decrease of CAT and APX and increased accumulation of H_2O_2 and TBARS (Donnini et al. 2011; Verma and Pandey 2016).

Enzymes coded by the CYP genes (designated CYP for cytochrome P450) are involved in fatty acid metabolism and biosynthesis of gibberellins (Hedden and Philips 2000), ethylene (Kende 1993) and jasmonic acid (Creelman and Mullet 1997). Cyclization of *ent*-kaurene, the first committed precursor of gibberellins, to ent-kaurenoic acid is catalysed by *ent*-kaurene oxidase (KO) which is a cytochrome P_{450}-dependent heme monooxygenase. Several 2-oxoacid-dependent heme dioxygenases are involved in the conversion of GA_{12} aldehyde to different gibberellins including their bioactive forms (GA_1, GA_4). Biosynthesis of jasmonic acid involves participation of iron enzymes lipoxygenase and allene oxide synthase (AOS). Overexpression of AOS gene in transgenics leads to increased production of jasmonic acid (Creelman and Mullet 1997). The terminal step of ethylene biosynthesis from 1-aminocyclopropane 1-carboxylic acid (ACC) to ethylene is catalysed by a non-heme iron enzyme ACC oxidase (Kende 1993). Martinis and Mariani (1999) suggested poor ethylene levels due to ACC oxidase inhibition resulted in sterile pistil formation. They reported that poor ethylene production due to iron deficiency in *naat* expressed in tobacco plants resulted in formation of abnormal pistil. Thus the role of iron may have far-reaching consequences in plant reproductive biology (Sun and Gubler 2004).

Involvement of iron in pollen-stigma interaction cannot be ruled out since iron is a constituent of peroxidase which is known to be enhanced for viable pollen germination (Bredemeijer 1979). McInnis et al. (2006) have identified class III peroxidase gene which is specific to stigma, SSP (stigma-specific peroxidase), and which is expressed in the receptive papillae of the stigmas of *Senecio squalidus* L. (Asteraceae). Since peroxidase genes are expressed in response to stress (Valerio et al. 2004), the localization of SSP in stigma papillae probably helps in pollen tube penetration and growth in the stigma by weakening the stigma wall. The SSP and stigma peroxidases may carry signals for species-specific pollen recognition by the stigmas. The high constitutive levels of SSP and peroxidase activity in stigmas (and style) may provide protection from pathogen attack (Do et al. 2003). Stigma peroxidases, such as SSP, impart a new role to ROS during reproductive stage for pollen-stigma interaction and protecting stigmas from microbial attack.

In a recent study, Takahashi et al. (2003) have shown severe suppression of reproductive development in transgenic tobacco plants lacking in synthesis of nicotianamine (NA). Nicotianamine plays a role in the chelation of the cationic micronutrients and their delivery to the reproductive tissues. Chlorotic leaves and abnormally shaped sterile flowers were observed in transgenic tobacco plants which expressed the NAAT (nicotianamine aminotransferase) gene. These anomalies were due to NA deficiency which was utilized in NAAT production in these transgenics. NA is required for normal reproductive development of the inflorescence, pollen grains and seed development. Vert et al. (2002) reported that NA-Fe could be transported to the floral organs by metal transporters. The heme-Fe is a constituent of allene oxidase involved in jasmonic acid synthesis, which is important for anther dehiscence (Kubigsteltig et al. 1999). This indicates another role of iron in plant

Table 2.3 Some enzymes in plants activated by manganese

Enzyme	Reaction catalysed
Superoxide dismutase (Mn-SOD)	$2\ O_2^{\bullet -} + 2H \rightarrow H_2O_2 + O_2$
NAD^+ -Malate oxidoreductase (malic enzyme)	Malate + NAD^+ + H^+ → pyruvate + NADH + CO_2
Phosphoenolpyruvate carboxykinase	Oxaloacetate + ATP → phosphoenolpyruvate + ADP + CO_2
Allantoate amidohydrolase (Mn containing)	Allantoate + H_2O→ uredoglycine + NH_3 + CO_2
Arginase	L-Arginine + H_2O → L-ornithine + urea
Glutamine synthase	Glutamate + NH_4 + ATP → glutamine + ADP + Pi

reproduction. NA also may regulate the iron in Fe-requiring protein such as DME (DEMETER) which is expressed for endosperm and seed viability (Choi et al. 2002).

2.3.2 *Manganese*

Manganese is a transition metal that exists in several oxidation states of which the most dominant oxidation state is manganese (Mn^{2+}) which is easily oxidized to the less stable manganic (Mn^{3+}) form. It functions as a cofactor or activator of several enzymes (Table 2.3). Manganese activation of enzymes accounts for its role in photosynthesis, carbohydrate metabolism, nitrogen metabolism and biosynthesis and metabolism of aromatic amino acids and secondary plant products (Burnel 1988).

The most significant role of manganese is in oxygen evolution as it is a constituent of the OEC (oxygen-evolving complex) associated with photosystem II (Hoganson et al. 1993). The complex associated with the PSII reaction centre contains a cluster of four manganese ions bound to the D1 protein (P_{680}). The Mn cluster functions as a mechanism for charge accumulation that enables it to oxidize the water molecule bound to it. In another role manganese enzymes NAD^+ malic enzyme and phosphoenolpyruvate carboxykinase play a critical role in decarboxylating the C4 acids to release CO_2 that can be fixed by Rubisco and incorporated in the carbohydrate pool (Hatch 1987).

Enzymes involved in glycolysis and gluconeogenesis have manganese as a cofactor. Thus it is involved in sugar metabolism. It functions as an activator of enolase and phosphoenolpyruvate carboxylase, catalysing terminal steps of glycolysis. The manganese enzyme phosphoenolpyruvate carboxykinase (PEPCK) catalyses the decarboxylation of oxaloacetate, produced during citric acid cycle, to phosphoenolpyruvate, which is finally converted to sucrose through a series of reactions. PEPCK acquires added importance in plants in which β-oxidation of lipids stored in seeds meets the energy requirement during early stages of seedling growth (Walker and Chen 2002).

Manganese is the cofactor of the first enzyme of the shikimate pathway that provides the precursors for the biosynthesis of aromatic amino acids – tyrosine, phenylalanine and tryptophan (Herrmann 1995). The reaction involves the condensation of phosphoenolpyruvate and erythose-4-phosphate to produce 3-deoxy-arbino-heptulosonate-7-phosphate (DAPH) catalysed by the Mn^{2+}-activated enzyme DAHP synthetase. Manganese-activated enzymes also figure in the biosynthesis of gibberellins and polyamines. Kaurene synthase, which is specifically activated by manganese, catalyses the production of *ent*-kaurene, the first committed precursor of gibberellins. Arginase, which catalyses the conversion of arginine to ornithine, is also activated by manganese. The latter is the starting material for the biosynthesis of polyamines. Manganese involvement in metabolism of phenolics and biosynthesis of lignins contributes to resistance against pathogen attack (Huber and Graham 1999).

Manganese functions in prevention of toxic effects resulting from ROS produced in response to environmental stresses. As a cofactor of the mitochondrial superoxide dismutase (Mn-SOD), manganese provides protection against oxidative damage. Inadequate supply of manganese produces oxidative stress in plants (Del Río et al. 1985; Kröniger et al. 1995; Yu et al. 1998; Yu and Rengel 1999). Transgenic tobacco overexpressing Mn-SOD in the chloroplasts exhibits improved tolerance to oxidative damage (Slooten et al. 1995). Yu et al. (1999) also observed the overexpression of genes for Mn-SOD in chloroplast or mitochondria as well as Fe-SOD in transgenic tobacco (*Nicotiana tabacum* L.), as compared to the non-transgenic. This overexpression enhanced the Mn-SOD activity and helped the plants to overcome oxidative stress induced by manganese deficiency.

Manganese has been assigned a role in providing protection to the nutrient-rich stigma. The role of Mn in providing protection to the receptive surfaces of stigmas from microbial attack in spite of its nutrient-rich secretions seems to draw analogy from the nectar in which microbial infection by ROS and H_2O_2 is protected due to the presence of a superoxide dismutase – Nectarin 1 (Carter and Thornburg 2004). Nectarin I (NEC1) is a germin-like protein (GLP) that has Mn-SOD activity. The Mn-SOD activity generates high level of H_2O_2 in the nectar which protects the female reproductive structures from attack by microbes and is expressed during nectar production prior to anthesis and ceases after floral pollination (Carter and Thornburg 2000, 2004).

2.3.3 Copper

Copper is an essential redox-active transition metal with high redox activity. It has two oxidation states – cuprous (Cu^+) and cupric (Cu^{2+}) – which are readily interconvertible. The less stable Cu^+ is readily oxidized to the stable Cu^{2+}. Like iron, copper has high affinity for oxygen (O_2) and readily binds to organic ligands. Copper is a structural constituent of important proteins and enzymes involved in various biochemical activities ranging from photosynthesis, respiration, reproduction and

Table 2.4 Copper enzymes in plants

Enzyme	Reaction catalysed
Polyphenol (catechol) oxidase	2*O*- Diphenol + $O_2 \rightarrow$ 2*O*- quinone + $2H_2O$
Laccase	2*p*-Diphenol + $O_2 \rightarrow$ 2-*p*-quinone + $2H_2O$
Ascorbate oxidase	2*L*-Ascorbate + $O_2 \rightarrow$ 2 dehydroascorbate + $2H_2O$
Monophenol monoamine oxidase (tyrosinase)	Tyrosine + dihydroxyphenylalanine + $O_2 \rightarrow$ dihydroxyphenylalanine + quinone + H_2O
Diamine oxidase (Cu containing)	$RCH_2NH_2 + O_2 + H_2O \rightarrow RCHO + NH_4 + H_2O_2$
Superoxide dismutase (Cu-Zn SOD)	$2\ O_2^{\bullet -} + 2H^+ \rightarrow H_2O_2 + O_2$

hormone signalling (Marschner 1995; Raven et al. 1999). Most copper in plants is complexed to proteins. Several copper-containing enzymes catalyse redox reactions (Table 2.4). As a constituent of the copper protein plastocyanin, copper links photosystem II to photosystem I (Katoh 1977). Plastocyanin activity is also involved in cyclic transport of electrons coupled to ATP production. Involvement of plastocyanin in electron transport accounts for decrease in photosynthetic rates and change in PSI/PSII rates in copper-deficient plants. A recent study with functional mutants of *Arabidopsis* suggested that decrease in photosynthetic rate of copper-deficient plants is caused due to poor transport of copper across the plastid envelope involving a P-type ATPase (Shikanai et al. 2003). Low rates of photosynthesis in copper-deficient plants could also result from structural changes induced in chloroplast organization and decrease in chlorophyll content and also leaf conductance to CO_2.

As a cofactor of several oxidases, including monooxygenases, copper plays a role in metabolism of quinones and phenols affecting synthesis of secondary metabolites including lignins. Inadequate supply of copper leads to decreased activities of copper enzymes – polyphenol oxidase, ascorbate oxidase and copper amine oxidase – which accounts for increased accumulation of phenolics in copper-deficient plants (Chen et al. 2002a, b).

Copper plays a protective role against abiotic and biotic stresses. Superoxide dismutase with Cu-Zn cofactor (Cu-Zn SOD) is localized close to the PSI complex (Ogawa et al. 1995) and catalyses rapid detoxification of superoxide ions ($O_2^{\cdot -}$) generated under photoinhibitory conditions (Fridovich 1995). Decrease in Cu-Zn SOD activity resulting from inadequate supply of copper weakens the antioxidant defence system of plants making them susceptible to oxidative damage (Yu and Rengel 1999). Copper involvement in lignin biosynthesis contributes to resistance against penetration of pathogens. Protection against pathogens is also offered by elevated levels of copper amine oxidases which generate reactive oxygen species that are cytotoxic to pathogens and activate defence mechanism of the host (Rea et al. 2002).

Copper plays an important major role in reproductive development of plants, which accounts for severe limitations in seed yield under copper deficiency. Several aspects of reproductive development are influenced by copper. Copper deficiency delays flowering and causes reduction in the number of flowers in large number of crops (Davies et al. 1978; Graves and Sutcliffe 1974; Reuter et al. 1981). Delayed flowering in Cu-deficient plants (Davies et al. 1978; Reuter et al. 1981) has been attributed to decreased polyphenol oxidase and ascorbate oxidase activity leading to accumulation of IAA which is inhibitory to flowering. Tanaka et al. (1995) reported that flowering in *Lemna paucicostata* 6746 and *Lemna gibba* G3 does not take place if the copper from the medium is chelated by the addition of EDTA. Deficient copper supply (<0.063 mg L^{-1}) in safflower (*Carthamus tinctorius* L.) delayed and impaired formation of the capitulum and the floret formed were totally sterile and failed to develop seeds (Pandey and Sharma 1999).

Development of anthers and pollen grains is very sensitive to plant copper status, and higher concentration of copper in anthers and ovaries than in other floral parts suggests involvement of copper in their development. The role of copper in microsporogenesis and pollen fertility may account for the more severe reduction in seed yield than dry matter production by copper-deficient plants (Graham 1975). Graham (1975) gave evidence for male sterility in copper-deficient wheat plants and showed that the deficiency interfered with development of pollen grain near the stage of meiosis of pollen mother cell and that decrease in seed setting is a function of male sterility and not ovule sterility. Inadequate supply of copper not only limits the size of anthers (Graham 1975; Agarwala et al. 1980; Dell 1981) but also prevents their dehiscence. Pollen sterility and impairment in development of endothecium were consistently observed by Dell (1981) in plants such as wheat, oat, barley, sweet corn, sunflower, petunia and sub-clover, grown under Cu-deficient conditions. They observed that at low copper supply, the inflorescences were developed, but flowers formed were male sterile showing either staminodes or arrow-shaped shrivelled stamen without tetrads and reduced lignification. They attributed the failure of anther dehiscence in copper-deficient plants to poor lignification of anther cell walls resulting from decrease in activity of copper-containing enzymes involved in biosynthesis of lignins.

Jewell et al. (1988) reported the formation of a non-functional tapetum in the anthers of copper-deficient barley plants which was expansionary and failed to supply nutrients to the developing pollen grains. Abnormal (polyploid) pollen grains were observed in copper-deficient plants of durum wheat (Azouaou and Souvré 1993). In copper-deficient wheat, number and size of pollen grains is severely restricted, pollen grains lack dense cytoplasmic contents and the high starch content, characteristic of normal, viable pollen grains (Agarwala et al. 1980; Jewell et al. 1988). Pandey and Sharma (1996) observed decrease in germination and changes in ultrastructure of pollen grains of green gram following copper deprivation which were minimized on copper resupply.

2.4 Zinc

Zinc has a single valency state (Zn^{2+}) which makes it different from the other redox-active micronutrients. The zinc ion (Zn^{2+}) binds to nitrogen- and sulphur-containing ligands through ionic bonds forming a tetrahedral geometry. Zinc is stable in the biological medium since it is inert to oxidation-reduction, and therefore it has a number of structural and physiological roles in plants (Pandey 2010b). An important role of zinc is maintenance of the structural integrity and permeability of plasma membranes. According to Bettger and O'Dell (1981), loss of membrane integrity is the earliest biochemical change caused by zinc deficiency. The involvement of zinc in the permeability of plant plasma membranes was first shown by Welch et al. (1982). In plants that are not adequately supplied with zinc, the root plasma membrane shows loss of structural integrity and enhanced leakage of ions. This is attributed to low concentration of phospholipids and thiol (-SH) groups in membranes of zinc-deficient plants (Rengel 1995), possibly because of zinc involvement in protection of thiol groups.

Zinc serves as a structural or catalytic cofactor for many proteins. It is a cofactor of a multitude of enzymes that regulate various metabolic activities in plants. The zinc proteins, of which over 300 are known, function as enzymes, transcription factors and regulatory proteins (Coleman 1992). The nature of binding sites in Zn^{2+}-ligand complexes determine activity of enzymes. The three Zn^{2+}-ligand binding sites are structural, catalytic and co-catalytic (Auld 2001; Maret 2005). Four ligands, generally cysteine (Cys), forming a tertiary structure of high stability are observed in structural site, e.g. alcohol dehydrogenase and protein kinase. The catalytic function of Zn enzymes is determined by the catalytic sites in which histidine and Zn are complexed with water and S, N or O as donors as in carbonic anhydrase, carboxypeptidases, etc. In co-catalytic sites, besides His, two or three Zn^{2+} are also bridged by amino acid residues (aspartic acid or glutamic acid) and a water molecule (Broadley et al. 2007). Some important enzymes with Zn^{2+} cofactor and reactions catalysed by them are listed in Table 2.5.

Zinc is also involved in stabilizing the protein of the DNA-binding domains of regulatory proteins or transcription factors. The Zn-binding domains have been termed as 'Zinc finger' and are widespread in nature. The 'Zinc fingers' function in folding of subdomains of regulatory proteins enabling them to recognize and bind to specific DNA sequence, inducing gene expression (Coleman 1992). The term 'Zinc finger' represents the sequence motifs in which Zn is coordinated between two cysteines and two histidines forming a compact nucleic acid-binding domain. Higher plants have about 30 C2H2 'Zinc finger' proteins which have an important role in plant development such as leaf and lateral shoot initiation, flower development, gametogenesis and seed formation (Colasanti et al. 1998; Luo et al. 1999; Takatsuji 1999). Some of the important 'Zinc fingers' have been listed in Table 2.6.

Zinc also plays an important role in maintaining the oxidative status of the plants by detoxification of ROS, which are potentially damaging to membranes and are catalysed by superoxide radical-generating NADPH oxidase (Bray and Bettger 1990). Thus absence of zinc from biological membranes increases their oxidative damage. Zinc offers protection against cellular damage caused by over production of active oxygen species (AOS) (Cakmak 2000; Pandey et al. 2002). This is achieved by restricting overproduction of ROS and by their rapid detoxification. The former is caused by zinc inhibition of membrane-localized NADPH oxidase (Cakmak and Marschner 1988; Cakmak 2000), which catalyses production of superoxide ions.

Table 2.5 Some important Zn enzymes and their reactions

Enzyme	Reaction catalysed
Alcohol dehydrogenase	$CH_3CH_2OH + NAD^+ \rightarrow CH_3CHO + NADH^+ + H^+$
Glutamate dehydrogenase	L-Glutamate + NAD^+ $\longleftrightarrow$ α-ketoglutarate + NH_4 + NADH + H^+
Superoxide dismutase (Cu-Zn SOD)	$2\ O_2^{\bullet-} + 2H^+ \rightarrow H_2O_2 + O_2$
RNA polymerase	Nucleoside triphosphate → pyrophosphate + RNA
Alkaline phosphatase	Orthophosphoric monoester + H_2O → alcohol + orthophosphate
Phospholipase	Phophatidylcholine+H_2O→ choline + phosphatidate
Carboxypeptidase A	Peptidyl-L amino acid + H_2O $\longleftrightarrow$ peptide + amino acid
Ribulose bisphosphate carboxylase	D-Ribulose 1,5-biphosphate+CO_2 → 2,3- phospho-D-digylcerate
Fructose-bisphosphate aldolase	Fructose-1,6-bisphosphate $\longleftrightarrow$ dihydroxyacetone PO_4 + D-glyceraldehyde-3-PO_4
Carbonic anhydrase	$H^+ + HCO_3^- \rightarrow CO_2 + H_2O$
Porphobilinogen synthase (ALA dehydratase)	2δ-Aminolevulenic acid ⟶ porphobilinogen
Carbonic anhydrase	$H^+ + HCO_3^- \rightarrow CO_2 + H_2O$

The latter is caused by rapid dismutation of the superoxide ions to hydrogen peroxide by the chloroplastic superoxide dismutase (Cu-Zn SOD). If not effectively detoxified, the superoxide ions ($O_2^{\bullet-}$) are converted to even more toxic $^{\cdot}OH$ ions through Haber-Weiss reaction. Photooxidative damage in zinc-deficient plants could also result due to impaired photosynthetic CO_2 fixation. The inhibition of carbonic anhydrase (CA) activity in zinc-deficient plants leads to poor intercellular levels of CO_2 due to which CO_2 fixation is impaired. This accentuates photogeneration of ROS leading to photooxidative damage of chloroplasts in zinc-deficient plants. The oxidative damage under zinc deficiency could also be enhanced by the decrease in activity of H_2O_2-scavenging enzymes CAT and APX (Cakmak and Marschner 1993; Pandey et al. 2002b, 2012; Pathak et al. 2005, 2009).

Zinc plays an important role in photosynthesis in higher plants (Salama et al. 2006). Zinc deficiency effect on photosynthesis may involve changes in chloroplast structure, photosynthetic electron transport, CO_2 fixation ability and photochemical membrane function (Salama et al. 2006). The ability of zinc to be readily incorporated in the organic complexes of the cells tends to be more abundant in the chloroplasts, which affects the photochemical capacity of PS II (Chen et al. 2008). This may also be due to CA, a zinc metalloenzyme, which exerts a buffering action by mediating pH changes in the stroma and, thus, prevents the chloroplast proteins from being denatured.

The plant hormone auxin (IAA) is essential for growth and development of organ primordial, from leaves to flower organs (Reinhardt et al. 2000). Zinc is essential for the synthesis of tryptophan the precursor of IAA (Alloway 2004; Nahed et al. 2007). Besides growth promotion, auxin is important for tropic movements like gravitrop-

Table 2.6 Some important 'Zinc finger' proteins involved in plant development

Proteins	Function	Expression	Plant species	References
COP1	Seedling development	Seedlings	*Arabidopsis*	Arnim and Deng (1993)
ZPT2-2, ZPT2-3	Floral recognition	Petal and stamen	*Petunia*	Takatsuji et al. (1994)
ZPT2-1Z ZPT2-1PT2-1				
SUPERMAN	Cell division in floral organ	Stamen primordial	*Arabidopsis*	Sakai et al. (1995)
CONSTANS	Promotes flowering	Apical meristem	*Arabidopsis*	Putterill et al. (1995)
AtZFP1	Photomorphogenesis	Shoot apex, apical meristem	*Arabidopsis*	Tague et al. (1997)
ZPT3-1, ZPT3-2	Gametogenesis	Tapetum, microspores, pollen and stomium	*Petunia*	Kobayashi et al. (1998)
ZPT4-1, ZPT4-2				
ZPT3-1, ZPT2-6				
SERRATE	Serrated leaf margins	Shoot meristem	*Arabidopsis*	Prigge and Wagner (2001)
EMF2	Flowering	Meristem	*Arabidopsis*	Yoshida et al. (2001)
TAZ1	Tapetum development	Tapetum	*Petunia*	Kapoor et al. (2002)
RIE1	Seed development	Embryo	*Arabidopsis*	Xu and Li (2003)
LIF	Axillary bud	Shoot branching	*Petunia*	Nakagawa et al. (2005)
MEZ1	Pollen meiosis	Anther	*Petunia*	Kapoor and Takatsuji (2006)
ZOS	Reproductive development	Panicle, seeds	*Oryza sativa*	Agarwal et al. (2007)
IMA	Flower and ovule development	Floral meristem	*Solanum lycopersicum*	Sicard et al. (2008)
ALSAP	Salt and drought tolerance	Leaf glands	*Aeluropus littoralis*	Saad et al. (2010)

ism, root initiation, apical dominance, fruit development and abscission. The growing regions with high auxin levels also had high concentration of zinc (Haslett et al. (2001) indicating their requirement for regulation of meristematic growth (Oguchi et al. 2004).

Zinc is critical for reproductive development of plants. Inadequate supply of zinc affects different aspects of reproduction – flowering, floral development, anthesis, gametogenesis, fertilization and seed maturation (Pandey 2010a). Under zinc deficiency, anther size and capacity to produce pollen are severely limited, and most pollen grains are sterile, which limits fertilization and seed setting. The pollen grains of zinc-deficient plants were found to be small in size and exhibited changes in the exine morphology which led to poor pollen viability (Sharma et al. 1990; Pandey et al. 1995, 2009). Besides aberrations in the pollen grain structure, zinc deficiency also induces changes in size, morphology and exudations of the stigma which inhibit pollen-stigma interaction (Pandey et al. 1995, 2006). The pollen receptive surface of the stigmatic head is reduced decreasing the area for pollen germination. A cuticle covers the stigmatic papillae due to which stigmatic exudates are not properly excreted leading to poor adhesion of the pollen grain, which prevents pistil in providing an extracellular environment conducive to adhesion and intracellular growth of the pollen tube through the stylar tract, culminating in fertilization. The rupture of cuticle requires activities of enzymes like cutinases and esterases (Dafni and Maues 1998; Hiscock et al. 2002), and the activity of these was found to be poorly expressed, whereas those of acid phosphatase which is inhibitory to pollen tube growth were found to enhance in stigma as well as pollen grains in zinc-deficient plants (Pandey et al. 2006, 2009, 2013). The involvement of zinc in reproductive biology has gained immense significance with zinc occurring as a constituent of ‘Zinc finger’ proteins. Several proteins that contain the TFIIIA-type ‘Zinc finger’ have been assigned regulatory functions in plant reproduction (Kubo et al. 1998; Takatsuji 1999). Thus SUPERMAN, CONSTANS, FIL, TAZ1 and ZOS have been implicated in the developmental regulation of various floral organs (Ayre and Turgeon 2004; Kapoor and Takatsuji 2006; Agarwal et al. 2007).

2.4.1 Molybdenum

Molybdenum is a metal of the second transitional series. It has four oxidation states, of which the most stable is the hexavalent form Mo (VI). Easy convertibility of different oxidation states of molybdenum enables it to participate in redox reactions (Mendel 2007). Over 30 enzymes catalysing oxidation-reduction reactions contain a molybdenum cofactor (Hille 1996; Mendel and Hänsch 2002; Sauer and Frebort 2003). The molybdenum cofactor (Moco) is in the form of a molybdopterin (MPT). The more important molybdenum enzymes of higher plants are listed in Table 2.7. The molybdenum enzymes also contain other cofactor(s), such as the Fe-S cluster,

Table 2.7 Molybdenum enzymes in plants

Enzyme	Reaction catalysed
Nitrate reductase	$NO_3^- + NAD(P)H + H^+ \longrightarrow NO_2^- + NAD(P)^+ + H_2O$
Xanthine dehydrogenase	Xanthine + O_2 + H_2O $\longrightarrow$ Uric acid + H_2O_2
Aldehyde oxidase	Oxidation of aldehydes (e.g. abscisic aldehyde) to corresponding acids
Sulphite oxidase	$SO_3^{2-} + H_2O \longrightarrow SO_4^{2-} + 2H$

heme and flavin (Bittner 2014). The molybdenum enzyme nitrate reductase has recently been shown to be a homodimer, each subunit containing three cofactors – a molybdenum cofactor (Moco), a β-type cytochrome (heme) and a flavin (FAD) – that are spatially arranged such that they form three distinct structural domains, each functioning as a separate redox centre catalysing a specific electron transport reaction (Campbell 1999).

As a constituent of prokaryotic nitrogenase, molybdenum is important for symbiotic N_2 fixation in leguminous as well as some nonleguminous plants (*Alnus glutinosa)*. The nodulating leguminous plants have a higher requirement of molybdenum than the non-nodulating plants because the former require molybdenum both for root nodule development and growth of the host (Ishizuka 1982).

Molybdenum is a cofactor of assimilatory nitrate reductase, and this results in accumulation of nitrate in plants grown with nitrate nitrogen. This is associated with reduced levels of protein and total organic nitrogen. Plants grown with reduced (ammonical) form of nitrogen do not show such effects, and their molybdenum requirement is also low. Molybdenum is also involved in ureide metabolism. Under molybdenum deficiency, the root nodules of ureide type of legumes (soya bean, cowpea) show enhanced accumulation of xanthine. This is possibly caused by low activity of the molybdenum enzyme xanthine oxidase (Schwarz et al. 2009).

Molybdenum nutrition has a significant role in plant reproductive development and seed yield. Molybdenum-deficient plants of maize show reduction in cob size, failure of styles (silk) to protrude out of the husk and poor seed set. Development of tassels and size of pollen grains are severely retarded, and most pollen grains fail to germinate (Agarwala et al. 1979). Phenomenal increase in yield of melon (*Cucumis melo* L.), following molybdenum fertilization of acid soils, that are low in molybdenum, suggests a role of molybdenum in pollen fertility. Molybdenum also effects seed development and vigour. Low molybdenum seeds have a low endosperm reserve and show qualitative change in seed proteins (Chatterjee and Nautiyal 2001). Low molybdenum seeds show premature sprouting or vivipary which can be controlled by foliar application of molybdenum (Cairns and Kritzinger 1992). Possibly the deficiency response is related to ethylene production involving the molybdenum enzyme aldehyde oxidase.

2.4.2 Boron

Boron is a metalloid and exists in several different forms, the most important of which is boric acid (H_3BO_3). It forms complexes with hydroxyl radicals of compounds having two closely situated $^{-}$OH groups in *cis* configuration. Important amongst these are the *o*–diphenols and sugars. The property of boric acid to form strong complexes with cis-diol groups (apiose and fucose) forms the basis for maintaining the structure of plant cell walls (Loomis and Durst 1992). Recent researches have provided evidence to show that boron forms covalent bonds with two monomeric rhamnogalacturonan II (RG-II) groups of the cell wall pectic polysaccharides to produce a dimeric rhamnogalacturonan II–boron complex (O'Neill et al. 2004). The borate ions are bound to apiose residue of the two RG-II monomers through a diester bond and function as an ubiquitous carrier of boron in higher plant cell walls. Boron cross-linking of cell wall RG-II provides the cell walls with a structure capable of turgor-driven growths. Boron requirement for cross-linking of RG-II in cell walls is specific and cannot be substituted by germanium (Ishi et al. 1999), which is known to substitute for boron in some other functions. Deficiency of boron prevents internalization of boron in cell walls (Yu et al. 2002). Boron is also important for membrane function. Its deficiency induces changes in membrane potential and H^+ extrusion (Blaser-Grill et al. 1989) resulting in impairment in membrane function (Cakmak and Romheld 1997; Pandey 2013; Archana et al. 2017).

The protection of the cell membranes from ROS may also stem from its role in maintaining the membrane structure (Cakmak and Romheld 1997). The role of boron in ROS-mediated cellular damage has been studied (Cakmak et al. 1995; Pfeffer et al. 1998; El-Shintinawy 1999; Liu and Yang 2000; Pandey and Archana 2013a, b; Archana and Pandey 2015a, b). Oxidative stress in plants maybe imposed by redox imbalance resulting from boron deficiency-induced changes in cell wall structure. Enhanced generation of toxic O_2 species in boron-deficient tissues can be expected as a result of enhanced production of quinones. Quinones produced by oxidation of phenolics can undergo one electron reduction forming a semiquinone radical. Subsequent reoxidation of the radical produces the superoxide radical ($O_2^{\cdot -}$) and further toxic O_2 species such as hydrogen peroxide (H_2O_2) and hydroxyl radical ($OH^{\cdot}$) (Appel 1993). In boron-deficient tissues, generation of toxic O_2 species can also result directly from phenolics during their oxidation. For example, enzymatic oxidation of catechin by mushroom tyrosinase and potato phenolase produced both O_2^- and H_2O_2 (Jiang and Miles 1993). Moreover, some polyphenols and quinones are known to be phototoxic and can be excited by light, producing toxic oxygen species such as singlet oxygen ($^1O_2$) and H_2O_2 (Bakker et al. 1983). Accumulation of phenolic compounds, particularly caffeic acid and quinones, which are highly reactive, leads to enhanced generation of the superoxide ions, which are known to cause peroxidative damage to cellular membranes. Cakmak and Romheld (1997) have described the changes in membrane structure and function under boron deficiency to peroxidative damage resulting from enhanced accumulation of the reactive phenolic compounds. Boron-deficient plants respond to oxidative stress by changes in antioxidative components. Increase in activity of antioxidative enzymes SOD, CAT and POD as observed in *Brassica* seedlings by Pandey (2013) has also been corroborated in earlier studies in boron-deficient (Cakmak and Romheld 1997; Kobayashi and Matoh 2004) and toxic plants (Karabal et al. 2003; Cervilla et al. 2007; Camacho-Cristóbal et al. 2008; Ardic et al. 2009; Archana and Pandey 2016). However recently Shah et al. (2017) observed that SOD, POD, CAT and APX decreased in boron-deficient and excess plants.

Boron is involved in the metabolism of carbohydrates. It affects the activity of key enzymes of the oxidative phase of the pentose phosphate pathway (PPP), viz. glucse-6-phosphate dehydrogenase and 6-phosphogluconate dehydrogenase. Both the enzymes show enhanced activities under boron deficiency and contribute to increased accumulation of phenolic compounds in boron-deficient plants (Pilbeam and Kirkby 1983). Low activities of phenolases in boron-deficient plants also contribute to enhanced accumulation of phenolics. The phenolic compounds, particularly caffeic acid and quinones, are highly reactive. Their excessive production enhances the generation of superoxide ions ($O_2^{\cdot-}$), causing peroxidative damage to cellular constituents. Boron involvement in ascorbate metabolism may also expose boron-deficient plants to oxidative injury. Boron enhances the activity of membrane-localized NADH oxidase (semidehydroascorbate reductase), which catalyses transfer of electrons to ascorbate free radical (Barr et al. 1993). Decrease in activity of NADH oxidase in boron-deficient plants could decrease ascorbate concentration, causing a decrease in antioxidative capacity (Lukaszewski and Blevins 1996).

Boron is important for nodule development as well as nitrogen fixation by leguminous plants. Boron-deficient plants show decrease in both. The early stages in nitrogen fixation are particularly sensitive to boron deficiency (Yamagishi and Yamamoto 1994). In the ureide type of nodulating plants (soya bean, cowpea), boron deficiency causes enhanced accumulation of allantoate, possibly because of inhibition in the activity of allantoate amidohydrolase, which catalyses the oxidative decarboxylation of allantoate.

Boron plays a significant role in plant reproduction. The boron deficiency has a more pronounced effect on reproductive yield than biomass production. The reproductive parts of flowers – anthers, ovary and stigma – possess a relatively higher concentration of boron than in other plant parts and show aberrations when plants are not adequately supplied with boron (Rawson and Noppakoonwong 1996).

Male gametogenesis has been reported to be particularly sensitive to low boron supply (Rerkasem and Loneragan 1994). Deficiency of boron can result in plants being functionally male sterile especially in cereals (Garg et al. 1979). However infertile pistil has also been reported (Coetzer and Robbertse 1987). Several studies have shown an involvement of boron in microsporogenesis and male fertility (Zhang et al. 1994; Rerkasem et al. 1997; Huang et al. 2000). In wheat under severe conditions of deficiency, anthers develop as small arrow-shaped structures largely devoid of cells in the anther locules and exhibit inhibition of floret fertility (Huang et al. 2000).

Anatomical investigation of pollen development in a boron-sensitive (SW41) and boron-insensitive (Sonora) wheat failed to detect any abnormality in pollen until after the uninucleate vacuolate stage, and pollen grains formed were sterile at anthesis (Rerkasem et al. 1997). The pollen grains in well-formed anthers appear empty, misshapen, shrivelled, or may be normal in shape but lack reserves of storage materials such as starch. Robbertse et al. (1990) reported that a gradient of boron concentration along the style facilitated the growth of pollen tubes. Shen et al. (1994) observed that the rate of pollen tube elongation was inhibited in boron-deficient plants. Pollen grain viability is impaired by boron deficiency especially the growth of the pollen tube (Pandey and Gupta 2013). This was also observed in in vitro studies carried out in pollen from boron-deficient plants (Wang et al. 2003; Archana and Pandey 2015b). O'Neill et al. (2004) reported that requirement of boron for pollen germination is related to the role of boron in stabilizing the RG-II structure present in the pectic polysaccharides which form the tip of the germinating pollen tube.

The boron-deficient oilseed rape showed morphological aberrations in stigmatic papillae and developed abnormal embryo sacs (Möllers 2017). Enhanced accumulation of phenolic compounds on the stigmatic surface due to boron deficiency inhibited the pollen germination in stigma of *Campsis grandiflora* (Dhakre et al. 1994). Iwai et al. (2006) showed that *NpGUT1* gene which encodes for glycosyltransferase involved in borate RG-II structure is expressed in the fertile reproductive structures. Another component of RG-II, 3-deoxy-D-manno-2-octulosonic acid (Kdo), is also required for pollen tube growth and elongation (Delmas et al. 2008). They observed that the Kdo-8-P synthase (*AtkdsA*2-V and *AtkdsA2-S*) gene expression produces effects similar to those induced by *NpGUT1* expression and further reiterates that pollen germination is governed by the RGII in the cell wall. Recently an increase in boron levels has been reported to enhance the induction of embryos in *Brassica napus* (Mahasuk et al. 2017).

2.4.3 Chlorine

Chlorine is a halogen element having only one oxidation state. It occurs in plants as a free anion (Cl^-) bound to exchange sites and as chlorinated organic compounds. Chlorine functions as a structural component of the manganese oxygen-evolving complex involved in charge accumulation and water oxidation by photosystem II (Merchant and Dreyfuss 1998). Another important function of chlorine in plants pertains to maintenance of turgor and osmoregulation. The osmoregulatory roles of chlorine include its involvement in turgor-driven growth of cells and stomatal functioning. Chlorine accumulates in relatively high concentrations in root and shoot apices, where it functions in the turgor-induced extension growth of cells. Chlorine deprivation of maize plants leads to inhibition in root elongation. Rapid growth of stigma, following anthesis in *Pennisetum americanum* L., is attributed to extension growths of cells resulting from increase in turgor caused by rapid mobilization of K^+ and Cl^- from the neighbouring cells (Heslop-Harrison and Roger 1986). In a recent study, stomatal response to enhanced concentration of CO_2 in fava bean leaves has been shown to be associated with enhanced flux of Cl^- from guard cells into the neighbouring apoplasmic fluid (Hanstein and Felle 2002). Enhancement of Cl^- flux is attributed to CO_2-induced activation of anion channels of the guard cell plasma membranes. Other examples of chlorine involvement in turgor-driven responses include seismonastic movement of *Mimosa pudica* and circadian rhythms of *Samanea saman* leaf movements. Chlorine also regulates the activities of certain enzymes. It is known to activate asparagine synthetase, which catalyses the glutamate-dependent synthesis of asparagine (Rognes 1980).

2.5 Conclusions

This article is based on the overview of available literature encompassing the physiological and biochemical roles of the nutrients in plants. The manifestations of the roles are discussed more in the light of the deficiencies of these nutrients since these are universally more prevalent and affect the yield and agricultural production of the crops. The nutrients like nitrogen, phosphorus, calcium and boron are structurally more important for the plants, whereas the other nutrients resulting in impairment in are constituents/prosthetic groups of enzymes and thus affect the enzyme-catalysed reactions of plant metabolism including macromolecule synthesis and biochemical reactions therein. They also help in proper cellular redox state and homeostasis of the plant system.

The extent of yield losses in plants strongly depends on the availability of the nutrient and its interaction with the soil and environmental conditions. In the present context for higher productivity, studies on the uptake and translocation mechanism and specially the transporters would be helpful to maintain the homeostasis of nutrients favourable for the yield. Several such studies on iron and zinc transporters have been fruitful, but more study is required. Research approaches involving protective mechanisms against environmental stress and molecular genetics and biotechnological tools need to be further explored to study how plants cope with low nutrient levels. This is especially important to meet the food demand which is increasing every year. Besides, nutrient biofortification which is a technique to elevate micronutrient levels and improve seedling vigour and yield is equally relevant. The genetic modification of crops to enhance nutrient fortification for human and animal nutrition welfare would be useful.

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Chapter 3
Foliar Application of Micronutrients in Mitigating Abiotic Stress in Crop Plants

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Abstract Balanced and precise crop nutrients application is a pre-requisite tool for meeting the second Sustainable Development Goals for achieving food security and improved human nutrition and to promote agriculture under stressful environments. Large increase in productivity cannot be attained without ensuring that plants are supplied with adequate and balanced mineral nutrients. Mineral fertilizers are an important basic resource for nearly half of the world's crop production. The productivity of food, feed, fiber, and biofuel is ought to be paralleled with global population that is expected to reach nine billion before the middle of twenty-first century. Among the nutrient management system, the foliar feeding provides a potential prospective option to meet the diversity of site- and crop-specific conditions, irrigation water supplies, eco-edaphic factors and farm management, and also concurrent economic and environmental prospective. Taking trade-off into account, the foliar feeding of essential nutrients will accrue in mitigating the negative effects of abiotic stresses, with concurrent maximizing productivity. This technique is cost-effective and beneficial under stressful conditions. The plants well-fed with essential nutrients have greater tolerance capacity in response to abiotic stresses. Thereby foliar feeding of nutrients is also referred as climate-smart agriculture. The response of foliar feeding varies greatly due to crop species, growth stages, concentration of added nutrient solution, and the relative water content in the plant parts. The plant nutrients, their importance in crop production, and some insights into how to best manage them by foliar feeding method in response to abiotic stresses are discussed.

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3.1 Introduction

The greatest challenges for agriculture sector over the coming decades will be to meet the food demand of ten billion people by 2050 in a sustainable manner around the globe. These are estimates that food production has to be increased by 70% over the existing productivity of crops by the year 2030 (Headey and Fan 2010). The goal can be materialized by bringing more land under plough and/or to enhance productivity per unit cultivated area by adopting modern crop husbandry practices, particularly adequate and balanced nutrition. In the recent times, the plant nutrition has been adopted as component of the 2030 Agenda for Sustainable Development, including 17 Sustainable Development Goals (SDGs) to offset the vagaries of environmental footprints for sustainable food and feed production. The farmers are on the frontline, which face tremendous challenges to harvest potential crop yield (FAO 2017). The ultimate goal of nutrient management is to provide an adequate amount of essential nutrients for a crop throughout the growing season. The soils vary greatly in their ability to provide nutrients in sufficient amounts that needs to be supplemented with either through soil and/or foliar application. For the sustainability of normal growth, health, and production of nutritious food and feed, plants require 17 essential nutrients out of total 92 natural elements in the plant system. Since the 1850s, mineral fertilizers have resulted in immense increase in agricultural production both in quantity and quality of food and fodder. However, intensive cultivation and non-replenishment of mined nutrients have resorted to widespread deficiency of nutrients in the plants. Among the essential nutrients, the micronutrients, viz., iron, manganese, zinc, copper, boron, molybdenum, chlorine, and nickel, are of equally important of micronutrients for mainstreaming functions of plant growth. Moreover, they cannot be substituted with other nutrients to perform specific physiological functions. The plants are always subjected to abiotic and biotic stresses throughout their lifespan. The abiotic stress causes substantial impact on the productivity of crops.

3.2 Abiotic Stresses

The growth and development of crop plants are affected to the greatest extent by virtue of abiotic stresses, i.e., high temperature, nutrient stress, radiation, heavy metal stress, drought, waterlogging, salinity, and environmental pollution (Table 3.1; Hasanuzzaman et al. 2012, 2013a, b, 2017a, b, 2018). The compound effects of these factors may cause reduction in the productivity ranging from 51% to 82%

Table 3.1 Economic yield loss due to different abiotic stresses

Stress	Crop	Growth stage	Yield reduction (%)	References
Drought	Maize	Low reproduction	47–87	Edmeades et al. (1999)
Drought	Rice	Grain filling	30–60	Basnayake et al. (2006)
Salinity	Tomato	Maturity	2.0–7.2	Qaryouti et al. (2007)
Salinity	Pearl millet	Maturity	15.1–60.1	Heidari and Jamshid (2010)
Heavy metal	Maize	Maturity	10	Guo et al. (2010)
Waterlogging	Grapes	Maturity	12.5–21.3	Zhou and Lin (1995)
UV stress	Soybean	Maturity	20	Teramura et al. (1990)
Heat stress	Wheat	Grains/ear	40	Ferris et al. (1998)

under different ecologies. Among these factors, temperature and drought produce profound effects on productivity than any other ones (Suzuki et al. 2014).

3.3 Stress Sensing in Plants

Plants contain practically 92 natural elements, but 17 elements have been recognized as essential nutrients that are required for plant growth. Three of these, carbon (C), hydrogen (H), and oxygen (O), are used in the greatest quantities, which are provided by the air and water. Other than these, nitrogen (N), phosphorus (P), and potassium (K) nutrients are regarded as macronutrients which are used in large quantities. The sulfur (S), calcium (Ca) and magnesium (Mg) are secondary nutrients which are no less necessary for plant growth than the macro-nutrients but are needed in somewhat small quantities. Concentration of these nutrients constitutes more than 0.1% of the total dry matter. The eight essential nutrients needed by plants in small amounts are called micronutrients, and these are iron (Fe), zinc (Zn), copper (Cu), manganese (Mn), molybdenum (Mo), chlorine (Cl), boron (B), and nickel (Ni). Generally, the concentration is found less than 0.01% of total dry weight (Table 3.2). The additional minerals, such as cobalt (Co), silicon (Si), aluminum (Al), sodium (Na), selenium (Si), iodine (I), and vanadium (V), have shown to be essential for certain plant species, but not required for all. The nonessential elements such as cadmium (Cd) and chromium (Cr) are detrimental to plant health (Jadhav et al. 2005).

The deficiency of micronutrients is called as “hidden hunger” and produces drastic effects on plant growth and development. Visually, plants show restricted growth, appearance of chlorosis, interveinal necrosis, and defoliation of leaves. The range between deficiency and toxicity is narrow for micronutrients (Brady and Weil 1999; Table 3.3). The sufficiency level of boron is 10–200 ppm, while the toxicity symptoms range from 50 to 200 ppm. The plants show similar toxicity symptoms for Fe and Mn (Yruela 2005). The acute deficiency of micronutrients results in reduced

Table 3.2 Essential and beneficial mineral nutrients for plants

Category	Nutrient	Symbol	Primary form of uptake	Main form in soil reserves	Relative no. of atoms in plants
Macronutrient	Nitrogen	N	Nitrate, NO_3^-, ammonium, NH_4^+	Organic matter	1 million
	Phosphorus	P	Phosphate, HPO_4^{2-}, H_2PO_4	Organic matter, minerals	60,000
	Potassium	K	Potassium ion, K^+	Minerals	250,000
	Calcium	Ca	Calcium ion, Ca^{2+}	Minerals	125,000
	Magnesium	Mg	Magnesium ion, Mg^{2+}	Minerals	80,000
	Sulfur	S	Sulfate, SO_4^{2-}	Organic matter, minerals	30,000
Micronutrient	Chlorine	Cl	Chloride, Cl^-	Minerals, rainfall	3000
	Iron	Fe	Ferrous iron, Fe^{2+}	Minerals	2000
	Boron	B	Boric acid, H_3BO_3	Organic matter	2000
	Manganese	Mn	Manganese ion, Mn^{2+}	Minerals	1000
	Zinc	Zn	Zinc ion, Zn^{2+}	Minerals	300
	Copper	Cu	Cupric ion, Cu^{2+}	Organic matter, minerals	100
	Molybdenum	Mo	Molybdate, MoO_4^{2-}	Organic matter, minerals	1
	Nickel	Ni	Nickel ion, Ni^{2+}	Minerals	1

Table 3.3 Location of nutrient deficiency symptoms on plants

Nutrient	Location of symptoms	Chlorosis?	Leaf margin necrosis?	Leaf color, shape
N	All leaves	Yes	No	Yellowing of leaves, leaf veins
P	Older leaves	No	No	Purplish patches
K	Older leaves	Yes	Yes	Yellow patches
Mg	Older leaves	Yes	No	Yellow patches (in oil palm) or interveinal chlorosis (in rice and maize)
S	Young leaves	Yes	No	Yellow patches
Mn, Fe	Young leaves	Yes	No	Interveinal chlorosis
B, Zn, Mo	Young leaves	–	–	Deformed leaves

seed germination (Ouzounidou et al. 1992), photosynthesis (Nussbaum et al. 1988), biosynthesis of chlorophyll (Munzuroglu and Geckil 2002), and inhibiting plant growth (Rehman and Iqbal 2007) and finally under extreme abiotic stress condition causes death of the plant (Sett 2017). The micronutrients are either mobile or immobile in their characteristics in plant system. Micronutrients Mo and Mg are mobile, and their deficiency appears on the older or lower leaves, while, Fe, Cu, Mn, Ni, and B are immobile, and their deficiency appears in younger upper leaves (Chapin 1980).

3.4 Strategies to Improve Tolerance

3.4.1 Nutrient Stress

The plant nutrient forms the basis for the livelihood of the plant. The deficiency and excessive quantities of nutrients are both detrimental for plant growth. Among nutrients, nitrogen stress produces greatest impact on the continuity of plant growth (Drenovsky et al. 2012). The photosynthetic activity and seed yield of chickpea were increased by foliar spray of nitrogen at the onset of drought condition (Palta et al. 2005). The tolerance was improved substantially with the foliar spray of potassium against various abiotic stresses (Ashraf et al. 2013). The deficiency of micronutrients mainstreams the physiology of plant species (Marschner 1995; Mengel et al. 2001). Boron deficiency reduces grain yield of wheat (Rerkasem and Jamjod 2004), chickpea (Johnson et al. 2005), and lentil (Srivastava et al. 2000), while the rice yield is affected substantially because of zinc deficiency (Wissuwa et al. 2006; Rehman et al. 2012).

The foliar spray of potassium not only enhances tolerance but also maintains osmotic potential, water uptake, and regulating stomatal closure (Waraich et al. 2011). It also facilitates in osmotic adjustment at lower water potential and thereby improves the ability of plants to tolerate drought conditions (Ashraf et al. 2013). There are evidences that water uptake was improved by foliar spray of potassium under water stress and thereby resulted in maintaining turgidity and regulation of stomata (Waraich et al. 2011). The nutrient use efficiency and uptake of nutrients from the soil are affected by phosphorus supply. It works in conserving and transferring energy in the cell metabolism (Jin et al. 2012). The drought stress could be lessened by foliar spray of zinc sulfate under drought conditions. The availability of added nutrients in the calcareous soils is very low and produces a little effect on the improvement of growth and development. Therefore, the foliar application of micronutrients is highly effective in correcting nutrient deficiency (Kabir et al. 2014).

3.4.2 Salt Stress

The salinity stress is the potential limiting factor for sustainable crop production. The salts may decrease production ranging from 20% to 50% in most arable crops (Shrivastava and Kumar 2015). The salinity has encroached about 33% of the irrigated agricultural land in the world. Moreover, the salinization of land is in order of 10% per annum because of low precipitation, higher evaporation, saline irrigation water, and poor agronomic practices (Jamil et al. 2011). The salinity affects germination, vegetative and reproductive growth, ionic toxicity, osmotic stress, and nutrient imbalance in the plant system (Bano and Fatima 2009; Hussain et al. 2018). The salinity produces negative effects on photosynthetic process (Netondo et al. 2004) and reproductive development (Munns and Rawson 1999; Table 3.4). Salt stress causes negative effects on metabolic processes, i.e., nutrient uptake, photosynthesis process, and synthesis of protein and nucleic acids. The adverse effects are manifested by low osmotic potential of soil solution, nutrition imbalance, and higher concentration of nutrients in the rhizospheres and ultimately reduce uptake of nutrients by plants (Ashraf 2001). Under saline condition, the plants experience deficiency of micronutrients, because of lower solubility of ions and thereby their lowered uptake by plants (Marshcner and Romheld 1994).

The occurrence of salt-induced changes in plant system could be ameliorated by foliar application of nutrients (Noaman et al. 2004). The reason being that exogenously applied nutrients are easily available to plants compared to soil applied and, moreover, are not fixed or diluted in the large volume of soil (Baloch et al. 2008). The foliar application of micronutrients results in enhanced uptake of macro- and micronutrients from the rhizospheres because of proliferation of root growth (Abdalla and Abdel-Fattah 2000).

3.4.3 Waterlogging

The plants are confronted with transient or permanent waterlogging in their lifespan. Various physiochemical processes, e.g., hypoxia, and osmotic stress hamper plant growth and root inhibition. The plants under waterlogged condition accumulate ethanol, which produces negative effects in various processes (Hasanuzzaman et al. 2017a). The lack of oxygen and deficiency of micronutrients causes reduction in the growth and development (Ashraf 2012).

3.4.4 Drought

The establishment of seedling and poor crop stand is affected due to water stress (Kaya et al. 2006). Under severe water stress, various physiological, biochemical, and morphological events are disrupted (Nonami 1998; Hasanuzzaman et al. 2017b; Tables 3.5 and 3.6). The drought reduces productivity of crops and stomatal closure and reduces respiration, uptake of nutrients, overproduction of reactive oxygen species, deterioration of cell membranes (Foyer and Noctor 2003; Ullah et al. 2017), and alteration in partitioning of assimilates among different organs. The combined effects of salinity and drought cause oxidative stress, due to restricted nutrient uptake from the medium (Fahad et al. 2015). The crop fed with adequate amount of nutrients has greater ability to tolerate drought stress (Osakabe et al. 2014).

Table 3.4 Foliar application of micronutrient on crops facing salt stress

Foliar application of micronutrients	Crop	Affected parameters	References
Zn, Fe	Sweet basil	Increased biomass, plant height, essential oil	Said-Al Ahl and Mahmoud (2010)
Fe, Zn, Mn	Wheat	Increased growth, nutrient uptake	El-Fouly et al. (2011)
Fe, Mn, Zn	Tomato	Increased growth, nutrient uptake	El-Fouly et al. (2002)
Mn	Barley	Increased growth, net photosynthetic rate	Cramer and Nowak (1992)
Se	Eggplant	Increased growth, yield, N P K level	Abul-Soud and Abd-Elrahman (2016)
Se	Canola	Increased yield, photosynthetic pigment content, improved the quality of canola oil	Hashem et al. (2013)
Se	Lemon balm	Increased growth, photosynthesis, amino acid, peroxidase, glutathione peroxidase	Habibi and Sarvary (2015)
Se, Si	Canola	Increased chlorophyll, MDA, proline, anioxidents, RWC, photosynthesis, oil percentage	Bybordi (2016)
Zn	Rice	Increased photosynthetic rate, transpiration rate, stomatal conductance, water use efficiency, total soluble protein, amino acid	Ashraf et al. (2014)
B. Mn	Sunflower	Increased growth, yield	Jabeen and Ahmad (2011)
Ca $(NO_3)_2$. $4H_2O$ (25%), K_2HPO_4.$12H_2O$ (21%), $MnSO_4$.$4H_2O$ (18%)	Rice	Increased water potential, osmotic potential, K^+/Na^+ ratio, leaf area, dry matter, growth stage, yield (18%)	Sultana et al. (2001)
KOH	Sunflower	Increased biomass, K^+/Na^+ ratio, yield (7%)	Akram et al. (2007)
Ca $(NO_3)_2$. $4H_2O$ (25%)	Cowpea	Increased plant growth, ion uptake, chlorophyll fluorescence	Murillo-Amador et al. (2006)
Ca $(NO_3)_2$. $4H_2O$ (25%)	Strawberry	Increased biomass, chlorophyll content, yield (11%)	Kaya et al. (2002)
B	Canola	Increased straw and seed yield increased by 37%	Abid et al. (2014)
B	Rice	More number of tillers/plant, high yield	Mahmood et al. (2009)
Zn	Maize	Increased crop yield, 100-grain weight	Chaab et al. (2011)

Table 3.5 Impact of drought stress on various physiological parameters

Physiological responses	Biochemical responses	Molecular response
Recognition of root signals	Transient decrease in photochemical efficiency	Stress-responsive gene expression
Loss of turgor and osmotic adjustment	Decreased efficiency of Rubisco	Increased expression in ABA biosynthetic genes
Reduced leaf water potential	Accumulation of stress metabolites like MDHA, glutathione, Pro, Glybet, polyamines, and α-tocopherol	Expression of ABA-responsive genes
Decrease in stomatal conductance to CO_2		Synthesis of specific proteins like LEA (late embryogenesis abundant proteins), DSP (desmoplakin), dehydrins
Reduced internal CO_2 concentration	Increase in antioxidative enzymes like, SOD, CAT, APX, POD, GR, and MDHAR	
Decline in net photosynthesis		
Reduced growth rates	Reduced ROS accumulation	Drought stress tolerance

Table 3.6 Foliar application of micronutrient on crops facing drought stress

Foliar application of micronutrients	Crop	Affected parameters	References
Fe + Zn + Mn	Sunflower	Increased proline concentration, carbohydrates	Babaeian et al. (2011)
Fe	Wheat	Increased height of plants, RWC, proline, protein	Jalilvand et al. (2014)
Se	Wheat	RWC, leaf area	Teimouri et al. (2014)
Zn. B. Mn	Wheat	Increased grain yield	Karim et al. (2012)
Fe, Zn, Cu	Sunflower	Increased plant height, chlorophyll, seed diameter	Rahimizadeh et al. (2010)
Se	Wheat	Increased turgid pressure, transpiration rate, total soluble sugar, free amino acid, and antioxidant activity	Nawaz et al. (2015)
Zn	Soybean	Increased biomass, improved K, Ca, and Cu	Weisany et al. (2014)
ZnO, B_2O_3, CuO	Soybean and cucumber	Increased biomass, improved N, P, Zn	Dimkpa et al. (2017)
Zn, Fe, Mn	Soybean	Increased oil, protein, grain weight	Kobraee et al. (2014)
Fe	Fennel	Increased chlorophyll “a” and b,” relative water content, water potential (ψ_w), carotenoids, ascorbate peroxidase, seed yield, and plant dry mass	Mirjahanmardi and Ehsanzadeh (2016)
K	Wheat	Increased plant height, spike length, yield (21%)	Aown et al. (2012)

(continued)

Table 3.6 (continued)

Foliar application of micronutrients	Crop	Affected parameters	References
Fe + Zn + Mn	Sunflower	Increased proline concentration, carbohydrates, yield (5.5%)	Babaeian et al. (2011)
F2	Wheat	Increased height of plants, RWC, proline, protein	Jalilvand et al. (2014)
Se	Wheat	RWC, leaf area, yield (29%)	Teimouri et al. (2014)
N+P+K	Wheat	Increased yield components, grains/spike, 7% increased grain weight	Shabbir et al. (2016)
K	Wheat	Enhanced grain yield, number of tillers 1000-grain weight	Mehdi et al. (2001), Evans and Riedell (2006), and Aown et al. (2012)
Zn	Mung bean	Increased pod/plant, number of seeds/pod, seed dry weight	Thalooth et al. (2006)
N+P+K	Wheat	Yield components, grains/spike, 7% increased grain weight	Shabbir et al. (2016)
N+P+K	Sorghum	Increased yield by 122%	Waraich et al. (2011)

3.4.5 Ultraviolet Radiation

The plants are exposed to UV light, UV-C, (200–280 nm), UV-B (280–320 nm), and UV-A (320–400 nm), while UV-C radiation produces profound negative effects on growth and development. Among these, UV-B, being 1.5% of the total radiation, impacts greatly than any other forms of radiation. The severe radiation targets DNA, lipids, protein, and photosynthesis (Hollósy 2002). The sensitive crop species are more prone to obnoxious effects of UV radiation (Zlatev et al. 2012).

3.4.6 Heat Stress

The heat stress in plants is manifested with sudden rise of temperature by 5–7 °C in the surrounding environment (Table 3.7). The prolonged prevalence of temperature causes abnormalities in the physiological and biochemical processes, which lead to the reduced growth and development (Kelly et al. 2010; Hasanuzzaman et al. 2013c). Photosynthetic rate is affected severely, which affects in reduction in sink duration and development of shriveled and less grain weight (Shpiler and Blum 1990).

Table 3.7 Foliar application of micronutrient on crops facing temperature stress

Foliar application of micronutrients	Crop	Affected parameters	References
Zn, Mn	Maize	Increased antioxidants	Bradáčová et al. (2016)
Se	Wheat	Increased yield, photosynthetic pigments, antioxidants	Iqbal et al. (2015)
Se	Wheat	Increased biomass, chlorophyll, antioxidants	Chu et al. (2010)
Se	Sorghum	Increased growth, proline, ascorbic acid, enzymes	Abbas (2012)
Se	Sorghum	Increased photosynthesis, grain yield, antioxidants	Djanaguiraman et al. (2010)
Mo	Wheat	Increased superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX)	Songwei et al. (2014)
Zn, Fe	Wheat	Increased seed yield and quality	Habib (2009)

3.4.7 Heavy Metal Stress

Heavy metal stress causes substantial downscaling of physiological and biochemical processes (Da-Lin et al. 2011). The plants are unable to express their full genetic potential due to the toxicity of heavy metals (Yadav 2010; Ghosh and Singh 2005; Speir et al. 2003; Hasanuzzaman and Fujita 2012). The heavy metals (cobalt, copper, nickel, cadmium, chromium, zinc) coming from industrial effluents and spillage of petroleum products during their transportation are affecting productivity of agricultural land (Modi et al. 2013).

3.5 Role of Micronutrients

The micronutrients play a key role in analogous to macronutrients in mainstreaming normal functioning of plant processes. The crop fertilized with micronutrients along with macronutrients has greater ability to address environmental stresses (Tables 3.8 and 3.9).

3.5.1 Iron

Iron (Fe) in the soil is reduced to Fe^{2+} before it is taken up by the plant and is translocated in the form of ferric citrate. Its uptake is significantly affected by the presence of Mn^{2+}, Cu^{2+}, Ca^{2+}, Mg^{2+}, K^{+}, and Zn^{2+}. The iron element having an ability to undergo a valence change is tended to form the chelate complexes. It is involved in

Table 3.8 Foliar application of micronutrient on crops facing heavy metal stress

Foliar application of micronutrients	Crop	Affected parameters	References
Si	Rice	Increased growth, Mg, Fe, and Zn nutrition, and the contents of chlorophyll "a" malondialdehyde (MDA)	Wang et al. (2015)
		SOD, peroxidase (POD), catalase (CAT), and a lower GSH	
Si	Rice	Increased endogenous phytohormones, ATPase	Kim et al. (2014)
Si	Maize	Increased biomass and xylem diameter, mesophyll and epidermis thickness, and transversal area occupied by collenchyma and midvein	da Cunha and do Nascimento (2009)

Table 3.9 Micronutrients essential for plant growth and some of their sources and characteristics

Micronutrient	Sources for corrective action	Management functionality	Reference
Fe	Usually applied as a foliar spray in the form of chelates such as Fe-EDTA (9% Fe) or Fe-EDDHA (6% Fe)	For soil application, Fe-EDDHA has the advantage that it is more stable in neutral soils	Habib (2009)
Mn	Deficiency occurs mainly in slightly acidic to neutral soils. Both Mn sulfate (24–32% Mn) and Mn-EDTA (13% Mn) are water-soluble and quick-acting and are suitable for foliar or soil application	Mn oxides may be used as a means of increasing the reserves. Indirect improvement of the soil supply may be achieved using acidifying additives	Cramer and Nowak (1992)
Cu	Deficiency may most easily be corrected for a longer period by soil application as Cu sulfate or oxides, etc.	Chelates and neutralized Cu sulfate (25% Cu) are suitable for foliar spraying of deficient crops	Dimkpa et al. (2017)
Zn	Usually applied to deficient crops as a foliar spray of Zn sulfate (e.g., 23% Zn) or Zn chelate (e.g., Zn-EDTA)	High levels of P in the soil may result in reduced availability of Zn	Thalooth et al. (2006)
Cl	Usually found in the soil as the chloride ion (Cl^-). Most commonly, it is applied with K in potash fertilizer (KCl) or with other salts	It is easily leached in drainage water	Liu et al. (2003)

(continued)

Table 3.9 (continued)

Micronutrient	Sources for corrective action	Management functionality	Reference
B	As a prophylactic treatment for crops with high demands, soil application of borax (11% or 22% B) is advisable	Needs vary widely, the rate depending on the crop (0.5–2.0 kg/ha B); risk of a damaging surplus affecting a succeeding crop with a low requirement. A better distribution can be obtained by incorporating the boron in phosphate or multi-nutrient fertilizers. Polyborates seem to be superior to borax for foliar application (at about 1 kg/ha)	Jabeen and Ahmad (2011)
Ni	Nickel was confirmed as an essential plant nutrient in 1987	One of its essential functions is in the urease reaction in soil N nutrition. It is thought to be important to grain development and maturation and in the movement of Fe into plant cells and is a factor in grain quality	Liu et al. (2003)
Co	Cobalt has recently been considered for addition as the 18th essential nutrient for plants, but has not been "officially" recognized. For now, it is considered beneficial, but not essential	Cobalt is necessary for nitrogen (N) fixation occurring within the nodules of legume plants. In N-fixing bacteria, Co is a vital component needed to synthesize vitamin B12, which is necessary to form hemoglobin, which is directly related to successful N fixation in legume root nodules	Liu et al. (2003)

heme enzyme system which includes catalase, peroxidase, and cytochrome oxidase. The concentration varies from 20 to 600 ppm, and adequate amount is 100 ppm. In the redox system, it helps in photosynthesis, nitrate and sulfate reduction, and nitrogen assimilation. Iron in combination with molybdenum helps the plant to fix atmospheric nitrogen (Malvi 2011).

3.5.2 *Manganese*

Manganese (Mn) occurs in the form of Mn^{2+} and other easily reducible forms. Its availability in soil is affected by oxidation-reduction reactions, decarboxylation, and hydrolyte reactions. Its uptake by plant is metabolically mediated in the form of Mn^{2+}. Manganese is immobile element and is not translocated from one organ to another in the plants. The range of concentration is 10–600 ppm, and 50 ppm is considered as an adequate level. Manganese is involved in redox reaction with photosynthetic electron transport system. The chloroplast is greatly affected by Mn^{2+} deficiency, thereby results in interveinal chlorosis and retardation of growth. It helps in preventing lodging and disease tolerance (Jacobsen and Jasper 1991; Rae et al. 1991; Mengel et al. 2001; Weisany et al. 2013).

3.5.3 Copper

The concentration of Cu^{2+} ranges from 2 to 50 ppm in plants, and its uptake is in the form of Cu^{2+} from soil solution. The optimum level is 6 ppm, while its uptake is inhibited in the presence of Zn^{2+}element. It is involved in nitrogen, protein and hormone metabolism, photosynthesis, respiration, pollen formation, and fertilization. It participates in oxidation-reduction reaction, due to its valency change characteristic. Copper is a cofactor in protein and enzyme system (Yurekli and Porgali 2006; Shar et al. 2011). Deficiency causes chlorosis in younger leaves, stunted growth and delayed maturity, melanosis, and even fungal attack (Solberg et al. 1999). The production of cereal is greatly affected as a result of severe copper deficiency.

3.5.4 Nickel

Nickel (Ni) is an essential element for plant growth. Its value ranges from 0.05 to 5 ppm, while its requirement is less than 0.05 ppm. It is involved in seven enzymes, i.e., glyoxalases, peptide deformylases, Methyl-coA reductase, superoxide dismutase, hydrogenases, and ureases. Nickel works as cofactor to convert urea into ammonia ion, which is used as a source of nitrogen by plants. It is accumulated in plant organs and tissues (Liu et al. 2003; Zhu et al. 2014).

3.5.5 Molybdenum

Molybdenum (Mo) is absorbed by plants in the form of MoO_4^{2-} ion from soil solution; however, its uptake is reduced in the presence of sulfate ions. The concentration in plants varies from 0.10 to 10 ppm and optimum range is 0.10 ppm. It is translocated in the plant as molybdenum-sulfur amino acid complexes along with polyhydroxy compound. Its concentration is usually less than 10 ppm dry matter. The molybdenum enzymes including nitrogenase, nitrate reductase, xanthine dehydrogenase, aldehyde oxidase, and sulfate oxidase are activated by this element. It also works in nitrogen (N_2) fixation, nitrate reduction, and transport of nitrogen in plants. The nitrogen fixation in legumes is hampered due to deficiency of Mo (Yohe et al. 2016). The deficiency symptoms include pale leaves and scorched, cupped, or rossetted leaves.

3.5.6 Zinc

The amount of zinc (Zn) is generally 100 ppm in plant dry matter. Its uptake occurs in the form of Zn^{2+}. It is a constituent of more than 70 metabolic enzymes. It works in biochemical processes such as cytochrome, nucleotide synthesis, auxin, metabolism, and maintenance of membranes. The carbonic anhydrase enzyme is activated by Zn^{2+} ion. The enzymes such as alcohol dehydrogenase, oxidoreductases, hydrolases, transferases, isomerase, lyases, and ligases also regulated in the presence of Zn^{2+}. The application of zinc mitigated the negative effects of salt stress due to inhibition and uptake of Na^+ and/or Cl^- from the soil. The grain yield of wheat was improved by 16% through foliar feeding of zinc (Yruela 2009).

3.5.7 Boron

Boron (B) is present in an undissociated form in the soil solution and is taken up by plant in the form of H_3BO_3 and $B(OH)_3$. The amount of boron is generally 0.2–800 ppm and requirement is 20 ppm. It is relatively immobile in plants and is not component of other enzymes. Boron is involved in nucleic acid, protein and RNA metabolism, photosynthesis, and cell membrane stability. Deficiency of boron affects meristematic growth. It works in cell division, flowering, pollen germination, salt absorption, and water relations. The presence of B improves the uptake of K by plants (Malvi 2011). Its deficiency causes infertility, smalling of leaves, and poor yield (Davis et al. 2003). In the absence of boron, there are no fertilization and production of seed in some crop plants. Zinc, copper, and boron are involved in synthesizing of lignin, which is used to strengthen cell walls of biological membranes (Osakabe et al. 2014).

3.5.8 Chlorine

Chlorine is absorbed in a large quantity in the form of Cl^- from the soil solution. Its uptake is metabolically controlled and sensitive to temperature and metabolic inhibitors. It is cofactor in oxygen-evolving enzymes concerned with photosystem II. It affects photosynthesis through stomatal regulation. Chlorine maintains cytoplasm at higher pH in the vacuole. It has the ability to fulfill osmotic and cation neutralization roles.

3.6 Foliar Feeding of Nutrients

Foliar feeding is being adapted as a regular farm management practices for increased growth and yield (Fernandez and Eichert 2009). There are evidences that yield potential and growth of crops could be improved to a greater proportion through foliar feeding of micronutrients in crops showing deficiency of nutrients (Rehm and Albert 2006). Foliar sprays of ferrous sulfate or chelates were found highly efficacious in correcting Fe chlorosis in wheat crop. There are estimates that 30% of world's cultivated soil is deficient in iron nutrient (Cakmak 2002). The total amount of Fe is much higher than its requirement by crop, but solubility in the form of its ferric citrate for uptake of plants is very low (Chen and Barak 1982). Under such edaphic conditions, it would be valuable to spray iron through foliage. The exogenous applied iron has been found useful in salt tolerance to sunflower and maize (Ebrahimian et al. 2010), increased concentration of iron in rice grain (Jin et al. 2008), and leaf chlorophyll in peach (*Prunus persica* L.). Foliar fertilization would prove efficient in crop having higher leaf area index for its quick absorption within a short time. Therefore, its efficacy can be increased by spraying more than once (Fageria et al. 2009). The foliar feeding of nitrogen, phosphorus, and potassium improves the waterlogging tolerance in rapeseed (Ashraf et al. 2011a, b).

3.7 Limitation in Quantity of Micronutrient Used for Foliar Application

The deficiency of micronutrients is corrected either through soil or foliar application. The rationale for the use of foliar fertilizer includes (a) the availability of soil applied nutrient is limited, (b) having loss of soil applied nutrients, and (c) environmental conditions limiting application through soil medium. Under these conditions, the decision for foliar application is determined by the magnitude of financial risk and gathering the yield target (Fernandez and Brown 2013). However, foliar application is considered with regard to performance of mineral elements, their rates of absorption, and mobility within plant organs (Fernandez and Brown 2013). For example, boron has equivalence to urea absorption but has limited translocation within the plant (Will et al. 2011). The translocation of boron is also limited in horticultural crops, and absorption is localized (Brown and Shelp 1997) while it is generally absorbed in cereal crops (Kutman et al. 2012). The foliar feeding of crop is being practiced extensively due to presence of high soil pH, salinity, and calcareousness of soils (Zhao et al. 2014). Recently, nanoparticles containing micronutrients are being effectively used for foliar application, which are cost-effective, and to avoid environmental pollution (Kumar et al. 2013) (Table 3.10). The size of nanoparticles is less than 100 nm; thereby, its decreased size results increased specific area of nutrients. The dissolution rate of low-solubility chemicals, e.g., zinc oxide, is increased (Alloway 2009).

3.8 Conclusion

The plant species always remain at war with the environmental conditions to complete their lifespan. The environmental vagaries include abiotic stress (temperature, heat, drought, mineral stress, heavy metals) and biotic stresses (diseases and insect

Table 3.10 Effect of foliar application of micronutrient on crops

Foliar application of micronutrients	Crop	Affected parameters	References
Fe + Zn + Mn	Sunflower	Increased proline concentration, carbohydrates	Babaeian et al. (2011)
Fe	Wheat	Increased plant height, RWC, proline, protein	Jalilvand et al. (2014)
Se	Wheat	Increased RWC, leaf area	Teimouri et al. (2014)
Zn. B. Mn	Wheat	Increased grain yield	Karim et al. 2012)
Fe, Zn, Cu	Sunflower	Increased plant height, chlorophyll, seed diameter	Rahimizadeh et al. (2010)
Se	Wheat	Increased turgid pressure, transpiration rate, total soluble sugar, free amino acid, and antioxidant activity	Nawaz et al. (2015)
Zn	Soybean	Increased biomass, improved K, Ca, and Cu	Weisany et al. (2014)
ZnO, B_2O_3, CuO	Soybean and cucumber	Increased biomass, improved N, P, Zn uptake	Dimkpa et al. (2017)
Zn, Fe, Mn	Soybean	Increased oil, protein, grain weight	Kobraee et al. (2014)
Fe	Fennel	Increased chlorophyll “a” and “b,” relative water content, water potential (ψ_w), carotenoids, ascorbate peroxidase, seed yield, and plant dry mass	Mirjahanmardi and Ehsanzadeh (2016)

pests). Among these stresses, the nutrient stress produces far greater impact on the growth and development of crop plants. The plants facing severe nutrient deficiency are highly prone to climate change and thereby cannot exploit their yield potential to their greatest proportion. The deficiencies of nutrient are being corrected through soil and/or foliar application during the active plant growth. The foliar spray is becoming common in most of the crops, where environmental conditions do not allow the farmers to apply fertilizers through soil medium.

The foliar spray is cost-effective and provides immediate remedial measures to correct the deficiency during certain growth stage. Thereby, the farmers could fetch greater harvest through foliar application of micronutrients, i.e., increased productivity from 10% to 20% across different horticultural and arable crops.

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Chapter 4
Biofortification of Plant Nutrients: Present Scenario

Sonal Dixit, Rajni Shukla, and Yogesh Kumar Sharma

Abstract A huge portion of global population is facing nutrient deficiency; particularly peoples of developing countries are the foremost sufferers. Although much development has been made till now, the problem of malnutrition seems to be unsettled. Recent estimates suggested that this problem will become more pronounced in the upcoming years. Unfortunately all of our key edible crops are deficient of certain vital micronutrients and vitamins which are crucial for normal growth, such as milled cereal grains which are deprived of lysine, vitamin A, folic acid, iron, zinc and selenium. Several strategies are there to enhance the quality and quantity of edible crops; among them biofortification seems to be an emerging tool to solve this malnutrition problem by elevating the concentration of bioavailable vitamins and nutrients. Biofortification is a cost-effective technique as there is only single time investment in research; it improves nutritional status of those crops which lack sufficient quantity of nutrients and is sustainable also because seeds and proliferation materials can be stored for long time. This approach owns great promise in achieving improved nutritional status of peoples and should carry on to be explored. The main focus of present chapter is to give a broad outlook of causes and solutions for micronutrient malnutrition in the world and also to discuss the current information, developments and future potential of biofortification for improvement of major edible crops.

Keywords Biofortification · Edible crops · Malnutrition · Micronutrients · Nutrient deficiency

4.1 Introduction

The nutrients which are the core substance for our body growth ultimately come from plants in the human diet. Foods provide calories for energy, in addition to which humans entail more than 40 nutrients and 20 minerals from daily food to

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keep themselves hale and hearty. Unfortunately, our meals are usually deficit of ample amount of these vital nutrients, which often give rise to under nutrition also termed as micronutrient malnutrition (Dutta et al. 2014). In developing countries like India, millions of people experience this insidious type of starvation of micronutrient malnutrition. Malnutrition is the most important reason of more than three million demises each year in the world. India is leading in having the largest number of malnourished people found in any single country. India, with a population of more than a billion, has about 48 million malnourished people (UNICEF 2009). Recent data from UNICEF shows that despite significant progress, about 42.5 million under 5 years are under weight. In India, malnutrition has been recognised as the major reason behind slow down progress in human development, and it also hampers the reduction in infant mortality (Measham et al. 1999).

This problem of malnutrition can be cured by enhancing the plant nutritional quantity and quality both. Plants can provide us these vital nutrients, and they obtain these from the soil or their growing medium. The study which deals with the chemical elements and compounds which are essential for the nourishment of plant, growth of plant, their metabolism and their external supply is known as plant nutrition. Besides carbon dioxide, water and oxygen, plants also need about 14 minerals for their sufficient growth. The list consists of macronutrients, calcium (Ca), magnesium (Mg), nitrogen (N), phosphorus (P), potassium (K) and sulphur (S), and the micronutrients, boron (B), chlorine (Cl), copper (Cu), iron (Fe), manganese (Mn), molybdenum (Mo), nickel (Ni) and zinc (Zn). Plant growth and crop yield were often affected by deficiency or low phytoavailability of any of these essential elements (Marschner 1995; Mengel et al. 2001). Enhancement and fortification of foodstuff have been used since decades, for instance, vitamin D added to milk or iodine to salt. Fortified food manufacturing is a long-term strategy that involves high costs to develop and test these food products before launching them in the market. Therefore they are very expensive and unaffordable to the majority of population.

Nowadays, scientists are very successfully using process of biofortification for enhancing plant's nutritional properties. Unlike conventional fortifications which involve the purchase of commercial food, biofortification of plant nutrients offers customers the ability to produce higher-nutrient foods. This is a relatively new concept, using multiple techniques to increase the nutrient content of edible food. Using certain techniques (genetical, breeding, biotechnological, physiological, agronomic, etc.), the plant traits are modified, or the absorption of nutrients from the soil and their accumulation in fruits or seeds (edible parts) are increased, and once these crop varieties are stabilised with these traits, they may be released. Hence, continued investment will no longer be required, and huge number of persons will be benefited from enhanced nutrition in agriculture products. Biofortification plays very vital role in improving nutrient value of staple food, which reduce the incidence of heart disease, anaemia, blindness, early mortality, etc.

4.2 Essential Micronutrients and Consequences of Their Deficiency

4.2.1 Iron

Iron is a vital nutrient for plants as well as humans. More than one-third of the world's population is suffering from anaemia, due to the deficiency of iron in human body (ACC/SCN 2000; Stoltzfus 2001; Tables 4.1 and 4.2); half of these cases are caused by dietary deficiency of iron (WHO 2001). Other than anaemia, deficiency of iron also adversely affects cognitive development, immune system, working capacity, efficiency and lot of problems in pregnant lady (Mayer et al. 2008).

4.2.2 Vitamin A

Vitamin A plays a very significant role in maintenance of vision of eyes, immune response, cell and bone growth, reproduction, development of embryo and adult gene regulation. Night blindness is a very common disease that occurs due to

Table 4.1 Consequences of micronutrient deficiency

Deficient micronutrient	Occurrence in developing country	Most affected groups	Consequences
Iron	2 billion	All but mainly women and children	Reduced cognitive ability, childbirth complications, reduced physical capacity and productivity
Vitamin A	250 million	Children and pregnant women	Increased child and maternal mortality, blindness
Zinc	1.5–2 billion	Women and children	Illness from infectious diseases, poor child growth, pregnancy and childbirth complications, reduced birth weight

Source: ACC/SCN (2000)

Table 4.2 Nutritional quality for mega-staple crops

Nutrient	Maize	Rice	Wheat
Calcium (Ca) (mg/100 g)	6	1	34
Iron (Fe) (mg/100 g)	3.45	1.46	3.88
Vitamin A (mg/100 g)	0	0	0
Vitamin C (mg/100 g)	0	0	0
Vitamin E (mg/100 g)	0.42	0	0.82
Niacin (mg/100 g)	3.63	1.49	6.37
Protein (g/100 g)	8.12	2.36	13.70

Source: Kumari et al. (2014)

deficiency of vitamin A (Mayer et al. 2008). Deficiency of vitamin A is common among the persons who preferably use micronutrient-deficient and carbohydrate-rich diets (Potrykus 2003).

4.2.3 Iodine

Iodine is an essential factor for the thyroid gland hormones, which mainly regulates the basal metabolic rate and also the growth and development of the body (WHO, FAO 1998; Lyons et al. 2004a). Iodine also have some of the combined function with selenium, iron and zinc (Lyons et al. 2004a, b; Zimmermann and Qaim 2004). It is reported that deficiency of iodine causes physical and mental retardation (WHO 2004).

4.2.4 Zinc

Zinc is an essential cofactor for the enzymes which are involved with RNA and DNA synthesis. Zinc deficiency commonly occurs in plants as well as humans and is responsible for diarrhoea, impairment of physical growth, low immunity, weak learning ability and inadequate repair of DNA damage which can lead to cancer (Hotz and Brown 2004; Prasad 2007). On average one-third of world's population is affected with zinc deficiency (Hotz and Brown 2004). The severity and frequency of dietary zinc deficiency have been acknowledged by WHO and FAO, and both have jointly recommended for the zinc fortification (Allen et al. 2006).

4.2.5 Calcium

Calcium is one of the most copious mineral elements in the human body, greater than 99% of which is located in the skeleton. Calcium maintain the rigidity and potency of the bones; along with this it is also concerned with several metabolic processes such as clotting of blood, cell proliferation, differentiation and linkage, muscle contraction and expansion, release of hormones and neurotransmitters, glycogen metabolism, etc. (Theobald 2005). Deficiency of calcium causes osteoporosis, a disease which is characterised by skeletal fragility and fractures.

4.2.6 Folate

Folates are vitamin B, extensive losses of which have been reported in boiled vegetables (Dang et al. 2000). Folate deficiency is related with a higher risk of cardiovascular diseases, impaired cognitive function and causes of cancer and also found associated with an increased risk of neural tube defects in newborns (Botto et al. 1999). Its deficiency is also related with megaloblastic anaemia in pregnant ladies and often intensifies the previously existing anaemia (Rush 2000).

4.2.7 Tocopherol

Tocopherols are vitamin E-containing chemical compounds. The rich sources of vitamin E are vegetable oils, for instance, oil from olive, corn, palm, sunflower and soybean. Nut products, whole grains, fish and green leafy vegetables also provide rich dietary supply of vitamin E. The antioxidant activity of vitamin E has proved its ability to prevent chronic diseases, especially an oxidative stress component such as cardiovascular diseases, atherosclerosis and cancer (Brigelius-flohe and Traber 1999).

4.3 Causes of Micronutrient Malnutrition

The prime reason of micronutrient malnutrition is intake of diets deprived of nutrients. People usually take high amount of staple food but consume very less amount of lentils, fruits, vegetables, fish and animal produce, which are major sources of bioavailable mineral elements and vitamins (CIAT/IFPRI 2002). The human body has no capacity to synthesise vitamins. Most of the atrophied are poor people whose major food are rice, as they cannot buy high-quality, micronutrient-rich food in large quantities because of its high cost. These people want to consume animal and fish products which contain rich supply of available micronutrients but are unable to meet the expense of this type of food. The plant foods like vegetables, fruits and lentils offer very dense supply of mineral elements and vitamins, but the rising trend of nonstaple food prices keeps them away from the reach of common people.

Nowadays, the cropping system has changed completely; the excessive use of cereals and cash crops and total reliance on cultivars which give high yield have resulted in remarkable decrease in food diversity as well as micronutrient intake. To make the most profit, farmers chose to grow high-yielding crops and use very few production technologies leading to a drop-off in the micronutrient and protein dense legumes (Pfeiffer et al. 2005). This trend is marked by a proportional decline in cereal cost and an increase in the cost of legumes, vegetables, fruits, animal and fish protein. It has been contributed considerably in micronutrient deficiency caused by these less nutritious cereal crops becoming readily accessible and more affordable.

4.4 Approach to Reduce Micronutrient Malnutrition

Poor people tend to eat large amounts of one or two staple foods daily that often contributes up to 70–85% of their total calorie intake. Such poor monotonous diets low in micronutrients lead to micronutrient deficiencies. There are three types of intervention to reduce such micronutrient deficiencies – food-based approaches for diversifying diets, distribution of supplements and public health interventions.

4.4.1 Dietary Diversification

For healthy life it is important to have an assorted diet whether it is a vegetarian or non-vegetarian diet; both may have similar concentrations for important nutrients, but their bioavailability may vary. For instance, the iron from a vegetarian diet is less accessible for absorption due to the dissimilarity in the heme and nonheme form of iron and also due to the presence of phytochemicals that allow or hinder iron absorption (Food and Nutrition Board 2001). Heme form of iron is more readily absorbed as compared to the nonheme form of iron present in foods (Roughead and Hunt 2000). Vegetarian diet is deprived of this available heme form of iron, and about 40% of non-vegetarian diet contain the iron in heme form. Although it is feasible to plan an iron-rich vegetarian diet, most estimations related to female vegetarians suggest that most people fail to do so, which results in much lower average iron intakes (11–18 mg/day) (Alexander et al. 1994; Perry et al. 2002).

4.4.2 Supplementation

Supplementation means stipulation of large dosage of micronutrients as medicine, directly in the form of tablets, capsules and/or syrups. These programmes have been extensively used in developing countries to supply iron, folic acid and vitamin A to the needy people like pregnant women, postpartum women, infants and children (Nantel and Tontisirin 2002; WHO 2009). World Food Programme (WFP), WHO and UNICEF suggested supplementation to be used in extreme conditions like in refugee camps to provide micronutrient as well as also in treatment of some diseases, such as in acute diarrhoea (Hotz and Brown 2004; WHO/WFP/UNICEF 2007). The circulation of vitamin A and iron supplements has most economical and successful programmes in the developing countries (Hunt 2002; Shrimpton and Schultink 2002). But, due to each year investment and requirement for highly trained health-care workers, certainly high cost involved in supplementation, and also there is a possibility of toxicity due to over-ingestion of supplements. These things make supplementation unsustainable.

4.4.3 Food Fortification

Food fortification means the adding up of more and more micronutrients in the processed food. This is one of the most worthwhile long-term schemes for enhancing mineral elements (Horton 2006). It has been used effectively since long back as a part of public health initiative for solving the problem of nutritional deficiencies which was a cause for extensive national public health problems (L'abbe et al. 2008). In the early 1920s, medical researchers announced that iodine could prevent goitre, which was widespread at that time. Iodisation of table salt reduced goitre incidence by 74–90% in the areas surveyed (Gomez-Galera et al. 2010). The success stories for food fortification are fewer for the rural poor and in developing countries since this strategy depends on the economic condition of the people to buy the product and the accessibility to the product (Parker et al. 2008). This approach has led to comparatively fast improvements in upgrading the micronutrient content of peoples. If help of available technologies and local distribution network is provided, this strategy will prove to be very cost-effective. However, in the absence of distribution networks, roads and shops, food product supplementation is simply ineffective in reaching the rural poor.

4.4.4 Agricultural Solutions

Agricultural solutions are the other means of reducing micronutrient malnutrition. The earlier described solutions improve the micronutrient in human diet by using diverse diets, supplements or modified food products, but agricultural solutions give a way to enhance the micronutrients directly in growing plants that produce the food products. This can be achieved by one of the following ways: fertilisation and biofortification.

Fertilisation is the process of supplying vital mineral elements to crops in the form of fertilisers to attain greater yields. It is mainly used for small-scale crop production and especially in areas with low phytoavailability. Macronutrient fertilisers containing nitrogen, phosphorus, potassium and sulphur and micronutrient fertilisers that consist of zinc, nickel, iodine, cobalt, molybdenum and selenium can cause significant effects on the accretion of nutrients in edible plant parts (Allaway 1986). Even though this strategy seems simple and inexpensive, it is doing well only in some cases of particular geographical area, due to the limitations of fertiliser and soil chemistry, together with the added complications of nutrient mobility and storage within the plant (Zhu et al. 2007). In soil zinc is found in mobile state, so the application of zinc sulphate will enhance the plant yield and also the zinc concentrations in legumes and cereals (White and Broadley 2005). For other important micronutrients such as iodine, nickel and selenium, enhancing soil-available supply of these micronutrients to edible crops can result in considerable increase in their amount in edible part of the plant (Graham et al. 2007; Hartikainen 2005). Similar to supplementation and fortification, agricultural intervention is probably more useful in niche conditions and when combine with other approaches (Cakmak 2008). In contrast, micronutrient elements like iron have not been successful to obtain a positive result using fertilisers because of low mobility of iron in soil (Fernandez et al. 2004; Grusak and DellaPenna 1999). For increasing concentration of iron in grains, foliar application of the iron-containing solutions is the only effective fertilisation practice (Rengel et al. 1999). Proper use of fertilisers also requires training by the applicators, to protect themselves and the rest of the environment (Graham 2003; Sors et al. 2005). Generally, these types of approaches cannot be universally applicable as a strategy to improve the nutritional quality of edible crops because these are appropriate to particular crops and minerals (Kendal 2009).

Biofortification is economical and environmentally feasible approach which can utilise either plant breeding or genetic engineering or both (Stein et al. 2008). It can supply micronutrients to a large number of persons at relatively very low cost (Nestel et al. 2006; Pfeiffer and McClafferty 2007). In addition, biofortification is more likely to reach all family members as staple crops are eaten by everyone and do not rely on proper implementation of a protocol (Bouis et al. 2000). Biofortified staple crops are also capable of serving the rural and urban poor, simultaneously, unlike the other micronutrient malnutrition intervention strategies (Nestel et al. 2006). Detail of biofortification approach for micronutrient enhancement is given below.

4.5 Biofortification

All of the previously mentioned solutions to micronutrient malnutrition suffer from some common problems. All require an annual investment, whether the investment is made by a governmental agency or non-governmental organisation (for supplementation schemes) or by private industry and the individual (for food fortification and fertilisation schemes). All require some degree of local infrastructure, to distribute the products to people that have been educated in their use. These limitations are major barriers to the implementation of sustainable solutions for malnutrition affecting those at the lowest end of the socio-economic scale. Biofortification is therefore an alternative reliable approach for improving mineral nutritional quality of crops and thus addresses micronutrient malnutrition in humans (Zhu et al. 2007). Perhaps the strongest argument for biofortification is the cost-effectiveness (Bouis et al. 2000), because investment is needed only once during the growth of the germplasm relative to ongoing costs associated with other strategies (Table 4.3) (Jeong and Guerinot 2008).

Table 4.3 Cost comparison between micronutrient malnutrition-reducing strategies, considering an US$ 80 million investment

Supplementation	Food fortification	Biofortification
Provides vitamin A supplementation to 80 million women and children in South Asia *for* 2 years, 1 in 15 persons in the total population, at a cost of 25 cents for delivery of each pill, each effective for 6 months	Provides iron fortification to 33% of the population in South Asia *for* 2 years. Costs of fortification are estimated to be 10 cents per person per year	Develops six nutrient-dense staple crops for dissemination to *the entire world's* people for consumption *year after year*. This includes dissemination and evaluation of nutritional impact in selected countries

Source: CIAT and IFPRI (2002)

Micronutrient bioavailability can be defined as the proportion of nutrient that is absorbed in the human body after storage, processing and cooking of the diet and is used for normal body function (White and Broadley 2005; Nestel et al. 2006). Biofortified crops must win over farmers by maintaining the yield productivity along with offering a benefit to health of human; micronutrient enhancement characters must be comparatively constant across diverse type of soil and climatic conditions and finally must meet consumer acceptance for taste and cooking quality (Welch and Graham 1999). Biofortified crops such as iron rice and golden rice hold a particular promise for India, as the people are predominately vegetarians. The massive Indian population must obtain their micronutrient content and vitamins through plants because of their vegetarian nature. Even if we succeeded in achieving a small increase in the plant nutrient contents, it will cause a great impact on the human health.

Biofortification has multiple advantages over the previously mentioned solutions:

- Biofortification takes advantage of increasing micronutrient in staple foods which are daily consumed on regular basis by all family members in a house. As staple foods dominate in the plate of poor people, this policy aims completely towards the low-income family (Nestel et al. 2006).
- This technique is a one-time investment, since, once the crop has been fortified, the seeds will fortify themselves.
- Biofortification is an advancement over fortification in case of providing nutrients to the deprived rural population because they hardly have any approach to obtain the nutrients from commercially fortified foods, by placing the means to the micronutrient malnutrition problem in the hands of the rural poor themselves (Yassir 2007).

4.5.1 Types of Biofortification

4.5.1.1 Conventional Breeding

The goal for most plant breeders has been to increase yield potential for their target crops. This has largely been accomplished by increasing yield but also via. the introduction of resistance genes for various diseases and pests. Attention has been given to improving crop quality, which can include improving nutritional content (WHO 2007). The effective biofortification programme should be able to reach the rural poor. The available genetic variation in vital nutrient content should permit breeding programmes to enhance the content of mineral elements and vitamins in crop plants (Cakmak 2008; Monasterio and Graham 2000). There are a variety of possibilities for improvement of micronutrient content through plant breeding, which include:

(i) Enhancement in micronutrient contents such as iron or zinc, or vitamins as beta-carotene
(ii) Reduction in the quantity of anti-nutrients, for example, phytic acid
(iii) Increasing the amount of sulphur-containing acids, which support the assimilation of zinc (Ruel and Bouis 1998)

It has been recommended to cross wild species with cultured varieties to increase the micronutrient concentration (Cakmak 2002; Monasterio and Graham 2000). Through mutagenesis new characters can directly be introduced in the required varieties (Raboy 2002).

4.5.1.2 Transgenic Approach

Conventional breeding-based biofortification strategy has not accomplished all the requirement and hence gathers very limited success). This technique of conventional breeding would require several years to attain noteworthy improvement in locally adapted plant varieties. The complications of the process also increase when breeding is concerned with more number of minerals and vitamins. Hence, an appropriate approach to improve these schemes is the introduction of genes encoding key enzymes using transgenic methods (Christou and Twyman 2004; Zhu et al. 2007). Plant transformation may be faster than the conventional breeding to achieve the nutritional target. Transgenic approaches can be a valid alternative, where breeding approaches are not successful (Brinch Pedersen et al. 2006; Zhu et al. 2007). The two primary limitations to biofortification via. transgenic crop improvement are lack of knowledge and regulatory difficulties. First, the transgenic approach requires genes with known functions to affect the trait of interest. In the absence of such knowledge, it is not possible to use plant transformation. Second and perhaps more important, regulatory issues greatly restrict the use of plant transformation for biofortification. These related regulatory obstacles with transgenic strategy make this technology commercially unviable (Johnson et al. 2007; Powell 2007). These problems also extend because of trade barriers and dissimilarity in national regulatory schemes, which hinder the manufacture, transportation and utilisation of transgenic produce (Ramessar et al. 2008). Developing countries like India and China are forced not to produce transgenic crops for the export, although they might be benefitted with the approach (Stein et al. 2008; Christou and Twyman 2004).

4.6 Utility of Biofortification in Present Scenario

Conventional breeding methods and biotechnological approaches can be helpful to bring the desirable changes in quantity and quality of micronutrient. The micronutrient contents can be enhanced by improving the content of desired micronutrient directly in cultivated crops or by the method of bioengineering. The nutritious crops which are unable to grow vigorously or which have dropped out during Green Revolution due to the enormous development made to cereals can be managed by bioengineering. Thus, it decreases the farm cost involved and improves the productivity and earning power of farmer along with meeting nutrient requirement (CIAT/IFPRI 2002). The requirement and demand of a biofortified food have to be sufficient to drive the product through complicated developmental stages and to equalise the associated expenditure. This purpose can be solved by publicising the health benefits of biofortified food clearly to the consumers. The following section shows few studies that have confirmed the nutritional value and cost-effectiveness of some biofortified crops.

4.6.1 Crops Rich in Iron

Iron-rich crops, for example, iron pearl millet, are enhancing the nutritional status of selected populations. The effectiveness of this iron-rich crop was estimated in secondary school children of Maharashtra, India. The children were fed twice in a day for 4 months with biofortified pearl millet flat bread, and a noteworthy enhancement in body iron content was observed in young boys and girls which were previously iron deficient. The children who were at the baseline of iron deficiency were significantly (64%) more likely to resolve their iron deficit problem in 6 months (Finkelstein et al. 2015).

4.6.2 Crops Rich in Vitamin A

Orange sweet potato (OSP) has the elevated levels of beta-carotene which is a building block for vitamin A. Studies conducted on the bioavailability of vitamin A showed efficient conversion of provitamin A to retinol, a usable form of vitamin A by the human body. Observations confirmed that an increase in consumption of provitamin A through biofortified crops as OSP resulted in increased beta-carotene concentration and also has a significant effect on vitamin A status of individuals. Analysis showed that 75% of the beta-carotene is retained in OSP even after its boiling during preparation of a meal. Intake of OSP has resulted in a considerable increase in vitamin A concentration among several age groups (Haskell et al. 2004;

Van Jaarsveld et al. 2005). Satisfaction of consumers and nutritional impacts of OSP have made this crop widely accepted.

4.6.3 Zinc-Rich Crops

Biofortification study with zinc has confirmed that biofortified wheat contains zinc in bioavailable form which can readily be absorbed in human body (Rosado et al. 2009). Because of the limitations of the available zinc biomarkers in evaluating the alteration in dietary zinc, research to discover more sensitive biomarkers are in progress these days.

4.7 Future Aspects of Biofortified Crops

As malnutrition is one of the major problems worldwide, biofortification along with conventional breeding and nutritional modification has become the first choice of the researchers for crop improvement in the future. To eradicate micronutrient malnutrition, biofortification is a promising and potential crop-based approach at present. Still, some essential exploration gap is present in existing biofortification technique, and currently it is a challenging venture (Singh et al. 2016).

- A wide knowledge gap exists between the bioavailability of micronutrients in food grain and mineral distribution pattern in plant system.
- The comprehensive perceptiveness of the mineral translocation mechanisms from soil to seed is missing in most of the edible crops.
- Before making the biofortified crops available to the customers, a detailed examination of its safety concerns is necessary.
- Some micronutrient loss that occurs during the processing of crops has not been analysed in majority of the crops which need to be investigated.
- Presently, the biofortification procedure is limited to a few important crops only and in some crops which have local significance. But to cope up with the micronutrient malnutrition, it is necessary to investigate all the crops which are related with the micronutrient deficiencies.
- Sometimes, enhancement of vitamins and micronutrient causes a negative impact on the colour and flavour of the finished product which was often not up to the standard of consumer expectations. Therefore, for greater adoption biofortified crops will be in acceptable form.
- The most important factor for malnutrition is the high cost of nutrient-rich food, so the biofortified crop has to be economically viable to common people.

Some of the important strategies to deal with these problems of biofortified crops would lie in molecular cytogenetics, in which through gene transfer, zinc and iron contents can be increased (Nestel et al. 2006). The drop-down in the micronutrient content during postharvest processing can be minimised by uniform allocation of minerals in the grain. To improve the bioavailability of micronutrients, manipulation of phytic acid level should be done during biofortification of crops (Nestel et al. 2006). The accomplishment of biofortification programme is directly related with the introduction of improved policies which must include agricultural policies, nutrition education, marketing and public awareness. Therefore, to completely eradicate the micronutrient malnutrition in human and further to ensure the food and nutritional safety, more organised steps towards the progress of biofortified crops together with appropriate alternatives for agronomic management are needed in the future.

4.8 Nutrient Biofortification and Abiotic Stress Tolerance

Productivity of crops and their quality have been adversely affected by several abiotic stress factors such as drought, frost heat, salinity and ion toxicities (Hasanuzzaman et al. 2012, 2017). Lack of micronutrients in agricultural soils is a fast-growing trend and is also an ever-increasing abiotic stress in agricultural world. Increasing the essential micronutrients by biofortification approach could be a significant alternative in enhancing the nutritional value and stress tolerance capability of crop plants. There are many evidences which showed that biofortification of nutrients in crops improved their resistance to abiotic stresses. Sufficient amount of silicon present in a large variety of plant provides them ability to resist in a stress environment (Ashraf et al. 2010). The benefits related with the increased content of vitamin B6, for instance, higher biomass and greater tolerance level to stress, suggest that improvement in the concentration of vitamin B6 could be a significant alternative for crop plants to improve the nutritional status and also to cope up with the abiotic stress (Vanderschuren et al. 2013). Some studies showed that biofortification of iodine leads to increased tolerance in some plants against specific type of abiotic stresses like heavy metal and salinity stress (Leyva et al. 2011; Gupta et al. 2015). Calcium is a crucial macronutrient for both plants and animals, associated with important structural and signalling function, deficiency of which can affect the crop quality and yield and also result in reduced resistance towards biotic and abiotic stresses.

To alleviate the stresses caused by several stress-inducing factors, concentration of reactive oxygen species increased in plants at their cellular level. Hence, the stimulation of antioxidants is acknowledged as a significant aspect of the adaptive response of plants leading to tolerance against stress (Gill and Tuteja 2010). Iodine was found to be the first inorganic antioxidants which give the ability to organism to mitigate stress level after the origin of oxygenic photosynthesis (Crockford 2009; Küpper et al. 2011; Venturi 2011). The treatment of temperature- and humidity-affected seeds of sunflower and soybean with calcium carbonate and iodine decreases the physiological deterioration rate and provides stress tolerance (Macias et al. 2016). Similar observations were also found with peanut seeds where pretreatment of seeds with zinc resulted in the increased tolerance of seeds to the fungal pathogen *Aspergillus niger* (Jajda and Thakkar 2012). Further investigations are needed on the prospective of micronutrients to increase the stress tolerance in plants. The advantage of biofortification is that it is more feasible from an economic perspective, accomplishing dual functions as a micronutrient enhancer and stress defender.

4.9 Conclusion

This chapter has tried to tackle the role of agricultural solutions and biofortification in addressing micronutrient malnutrition. In the future, mineral and vitamin deficiencies are likely to be more menacing, but the biofortification approach is emerging as a promising means to deal with this problem. Biofortification is a simple, cost-effective, crop-based strategy; that's why it gives assurance for coping up with the micronutrient malnutrition crisis and is best suitable method in the developing countries. But, the scientific approach alone is not sufficient, although a holistic approach is needed to cope up with the problem of micronutrient malnutrition. There is a need to generate awareness among people about the advantage of food diversity and suggesting them feasible solutions how they can improve their dietary requirement. Remarkable improvements have been already going on in this area; further suitable strategies and potential planned studies could result in biofortification's immense accomplishment in the near future.

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Chapter 5
Trace Elements in Abiotic Stress Tolerance

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Abstract Trace elements are minutely required elements for normal growth and functioning of biological systems. They perform several intricate roles in complex cellular phenomena including plant protection against stress conditions. The role of various trace elements in enhancing plant's tolerance to abiotic stresses is multifaceted. At primary level, they are the constituents of cell organelles and membranes and serve as metalloproteins and metal cofactors or activating agents for key ROS

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scavenging enzymes. At secondary level, they regulate key metabolic pathways involved in gene expression; biosynthesis of proteins, carbohydrates, and lipids; and production of phytohormones which protect plants from ROS-induced injury. The role of some important individual trace elements in enhancing plant's tolerance to various abiotic stresses is explained here in different plant species.

Keywords Trace elements · Abiotic stresses · Tolerance mechanisms · Biomolecules · Metal cofactors · Abiotic stress · Micronutrients · Oxidative stress · Phytohormones · Reactive oxygen species · Soil fertility

5.1 Introduction

Modern analytical techniques have confirmed the presence of a number of elements in biological tissues with specific designated functions. Some elements are major constituents of the cells and required in larger quantities such as carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorous (P), and potassium (K), while others are present in very small amounts like iron (Fe), copper (Cu), chlorine (Cl), magnesium (Mg), zinc (Zn), manganese (Mn), molybdenum (Mo), boron (B), cobalt (Co), selenium (Se), nickel (Ni), aluminum (Al), etc. Due to their lesser abundance in biological tissues and detection in trace amounts by earlier techniques, the minor components got several names in the earlier literature such as "minor elements," "oligo-elements," "oligo-metals," "micronutrients," "trace metals," and "trace elements." By definition, trace elements are minutely required elements to maintain normal growth, development, and biological functions in plants and other biota. However, some of the trace elements, commonly known as "heavy metals," have no known biological role in plants including cadmium (Cd), lead (Pb), and mercury (Hg); rather elevated levels of such metals may cause toxicity and injury in plants (Ali et al. 2014; Khan et al. 2014; Daud et al. 2009). In this chapter, trace elements having positive roles in plants are discussed with special emphasis on abiotic stress tolerance.

Importance of trace elements in higher plants has been previously judged by physiological and metabolic roles and deficiency symptoms (Maksymiec 1998; Cakmak and Kirkby 2008; Hajiboland and Farhanghi 2011). They play roles in a number of intricate cellular phenomena. Examples include but not limited to synthesis of biomolecules, formation of secondary metabolites, cell wall lignifications, stabilization of ribosomal fractions, primary and secondary metabolism, genes regulation, hormonal balance, ionic homeostasis, nitrogen assimilation, cell signaling, and protection of cells against biotic and abiotic stresses (Stiles 2013). Moreover, several key physiological functions in plants, such as regulation of stomata opening and closing, transport across xylem and phloem, and permeability of membranes, are all trace element-dependent mechanisms (Hänsch and Mendel 2009). To discuss here the physiological role of each trace element in great detail will be out of the scope of this chapter. Therefore, emphasis here is on the roles of trace elements in combating different abiotic stresses through various tolerance mechanisms.

Several factors may induce abiotic stresses in plants such as temperature, water, light, salinity, toxic chemicals, and heavy metals (HMs). They generate excess reactive oxygen species (ROS) in cells such as hydrogen peroxide (H_2O_2), superoxide anion ($O^{\bullet -}{}_2$), hydroxyl radical ($^{\bullet}OH$), and singlet oxygen ($^1O_2$), causing oxidative stress. The oxidative stress may affect synthesis of biomolecules such as DNA, protein, carbohydrate, and antioxidant network and may induce changes in cell wall morphology, biomembranes, peroxisomes, mitochondria, chloroplasts, ribosomes, peroxisomes, nuclear envelop, etc.

Plants have a complete set of defense mechanisms in the form of antioxidant enzyme and antioxidant nonenzyme components to tackle oxidative stress. Trace elements constitute and regulate plant defense systems. Some important antioxidant enzymes are catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD), peroxidase (POD), and glutathione reductase (GR). Nonenzyme components may include glutathione, ascorbate, phenolic compounds, and carotenoids. Besides antioxidant machinery, some other mechanisms may also be involved in circumventing abiotic stresses such as avoiding contaminant uptake, restricted-translocation of HMs, root exudation, metal chelation, and induction of stress-related proteins. Besides this, trace elements are the constituents of various cell organelles and part of several metabolic activities. They are constituents of basic biomolecules such as DNA, RNA, protein, lipids, and carbohydrates that directly or indirectly play role in plant tolerance to abiotic stresses.

Response of plants to abiotic stress is very complex, both at biochemical and genetic level. However, gene transformation and expression of stress conditions may provide an opportunity for building stress tolerance in plants. The task may be accomplished by manipulating the genetic make of the stressed-host plant and transferring single or multiple genes from wild-type or resistant plants to the desired plant. There may be several aspects in which genetic tolerance can be developed in stressed plants: firstly, by transferring genes related to cell signaling and regulatory pathways; secondly, by exploiting genes that encode enzymes of metabolic pathways related to structure and functions; thirdly, by exploiting genes that encode proteins involved in cell membranes and other proteins protection; and fourthly, by manipulating genes involved in maintaining ionic balance, i.e., aquaporins and iron transporter genes.

The role of trace elements in combating abiotic stresses is multifaceted. They are integral part of almost all cell compartments and metabolic activities. It has been suggested that the concentration of iron (F^{+2}) in cytosol remains between 10^{-7} and 10^{-6} M (Hider and Kong 2013). Similarly, chloroplasts contain 80% of the cell iron. These compartments have several key enzymes that play roles in plant protection against stress conditions. For example, mitochondria contain alternative oxidases (AOs) and NADPH dehydrogenase. Mitochondrial inner membrane, on both sides, possesses NADPH dehydrogenase. AOs and NADPH dehydrogenase, along with glutathione in mitochondria, help scavenge ROS. The roles of individual trace elements in combating different abiotic stresses are discussed in the following section in greater detail.

5.2 Role of Individual Trace Elements in Abiotic Stress Tolerance

5.2.1 Iron

Iron is a redox-active element found in two oxidation states. Its interchange between Fe^{+2} and Fe^{+3} oxidation states drives several metabolic reactions in plants including ETC. The Fe concentration of soils may range from 0.6% to 2% (Kabata-Pendias 2010). After plant uptake, Fe is mainly stored in the vacuoles and apoplastic regions and then transported to various cell compartments via copper transporters (Pilon 2011). Iron, in its free state, triggers ROS generation and causes oxidative damage; hence, it is complexed as Fe chelates in the cells and later released and transported to various cellular compartments under the influence of transporter genes. It is an integral structural part of the cell organelles. The Fe concentration in different cell compartments is variable; however, chloroplasts contain maximum Fe (80%).

Iron has potential role in photosynthesis, mitochondrial functioning, N assimilation, biosynthesis of hormones, and controlling ROS generation. It is also an important constituent of proteins: which on the basis of Fe legends are generally grouped into Fe-S cluster proteins, heme group proteins, and other Fe-containing proteins. Moreover, it is a constituent of nonheme proteins such as ferritins that contain 4500 Fe atoms per molecule and play a significant role in Fe balance and oxidative stress tolerance. Copper serves as cofactor for SOD enzymes which are important metalloenzymes distributed in various cellular compartments. SOD enzymes reduce $O^{\bullet -}{}_2$ into H_2O_2 and then to O_2 and serve as primary defense of plants against ROS-induced oxidative damage. SODs also reduce risk of $OH^{\bullet}$ formation. These enzymes are grouped into FeSOD, MnSOD, and Cu-Zn SOD. FeSOD is mainly found in chloroplasts and is further divided into homodimer and tetramer containing FeSODs: having two and four equal protein subunits, respectively. The homodimer FeSOD is made of 20 kDa subunit protein, while tetrameter has 80–90 kDa with 1–2 and 2–4 g atoms of Fe in their active centers, respectively (Alscher et al. 2002). Homodimer FeSOD is mainly found in microbes while tetramer FeSOD prevails in higher plants. However, in *Arabidopsis thaliana*, three FeSODs have been detected in which FSD2 and FSD3 contribute to chloroplast synthesis (Myouga et al. 2008).

The role of FeSODs, in conferring tolerance to abiotic stresses, has been highlighted in several transgenic studies (Van Camp et al. 1996; Van Breusegem et al. 1999b; Deák et al. 1999). These studies are either focused on transferring FeSOD gene from different plants and its expression in the host plant or transferring other genes related to abiotic stress tolerance and monitoring their effects on host antioxidant machinery such as FeSOD. In transgenic tobacco, overexpression of FeSOD gene protected plasmalemma and photosystem II (PS II) from methyl viologen (MV) (Van Camp et al. 1996). Similarly, overproduction of FeSOD enhanced tolerance against MV in transgenic maize (Van Breusegem et al. 1999b). In another study, cysteine proteinase inhibitor gene from *Oryza sativa* enhanced *Nicotiana tabacum* tolerance to drought, high temperature, and high light intensity stresses by elevating FeSOD and guaiacol peroxidase activities (Demirevska et al. 2010).

Iron is also an important constituent of heme proteins such as cytochromes and globins: synthesized in chloroplasts and mitochondria. In globins, nonsymbiotic hemoglobins, due to their affinity for oxygen, combat ROS and enhance plant tolerance to different abiotic stresses (Dordas 2009). Similarly, plant ferritins, the Fe-rich proteins mainly localized in chloroplasts, maintain free intracellular iron homeostasis to avoid Fe-induced hydroxyl radical formation and subsequent oxidative damage. Previously, overproduction of alfalfa ferritin enabled transgenic tobacco to withstand biotic and abiotic stresses (Deák et al. 1999).

5.2.2 *Copper*

Copper is structural and functional component of plant cells. It is needed for biosynthesis of chlorophyll and proteins, to maintain integrity of cell wall and chromosomes, cell respiration, carbon (C) and N metabolism, Fe homeostasis, and protection against oxidative stress. It is relatively immobile in plants and concentrated in chloroplasts with an average concentration of 10 μg g^{-1}, on dry weight basis. Copper deficiency may cause impaired vegetative and reproductive plant growth and disturbed metabolic pathways. Previously, Cu deficiency had caused disintegration of thylakoids and inhibition of PSII (Maksymiec 1998). It exists in multiple oxidation forms and entrusted with reducing and oxidizing properties. However, interchange of copper, in vivo, between its ionic forms, i.e., Cu^{+2} and Cu^{+1}, induces $OH^{\bullet}$ generation, causing damage to cell ultrastructure and biomolecules. Recently, copper chaperones have been identified which maintain Cu homeostasis and its routing to proteins whose function is dependent on Cu. This helps cells to avoid free Cu accumulation and subsequent damage to cellular compartments (Harrison et al. 2000).

Copper acts as redox catalyst for more than 30 enzymes involved in various metabolic pathways (Harrison et al. 1999). Plastocyanin, cytochrome *c* oxidase, and Cu-Zn SODs constitute principal Cu proteins in plant cells. Plastocyanin, found in chloroplasts, is vital for photosynthesis as it works as electron carrier between PSI and PSII. Cytochrome *c* oxidase, a transmembrane protein localized in mitochondria, is also involved in electron transfer that ultimately leads to H_2O and ATP synthesis. Based on localization, Cu-Zn SODs are grouped into chloroplastic and cytosolic Cu-Zn SODs, respectively. Chloroplastic Cu-Zn SOD is mainly found in stroma of the thylakoids while cytosolic Cu-Zn SOD is distributed in apoplastic regions and nucleus. Cu-Zn SODs help quenching ROS in plants. Response of Cu-Zn SOD is differential in tolerant and sensitive varieties of plants. Most of the earlier studies have reported increased Cu-Zn SOD activity in tolerant varieties. For example, the activity of Cu-Zn SOD was increased in salt-tolerant variety of *Setaria italica* when its seedlings were exposed to salinity stress (Sreenivasulu et al. 2000). Similarly, chloroplasts, isolated from salt-tolerant pea, demonstrated increased activities of Cu-Zn SOD as compared with sensitive varieties (Hernandez et al. 1995).

Transgenic plants, overexpressing Cu-Zn SOD genes, are potential subjects for inducing and studying tolerance mechanism in plants under stress conditions. In a previous study, rice's tolerance to MV and salt stresses was enhanced by transforming *Oryza sativa* with Cu-Zn SOD gene from *Avicennia marina* (Prashanth et al. 2008). Likewise, upregulated Cu-Zn SOD genes improved transgenic tobacco's tolerance to stress induced by low temperature and water deficiency (Faize et al. 2011). Moreover, downregulating microRNAs in *Arabidopsis thaliana* stimulated expression of Cu-Zn SOD genes under high light and MV stresses (Sunkar et al. 2006).

5.2.3 Zinc

Zinc is one of the most extensively used microelements in biological systems. Its deficiency is common among major field crops. Zinc-deficient plants exhibit symptoms like retarded growth, chlorosis, necrosis, and delayed seed development. That's why recent research is focused on fortification of major crops with zinc (Poletti et al. 2004; Lu et al. 2008). Numerous biological roles are attributed to Zn in plants such as stability of cell membranes, chlorophyll formation, protein synthesis and stabilization, enzyme activation, auxin regulation, etc. It is an integral part of approximately 1200 proteins: related to regulation of DNA, transcription, RNA synthesis and editing, and protein-protein interactions. A large family of regulating proteins containing Zn as Zn-finger motif plays important roles in tolerance to abiotic stresses (Yang et al. 2009).

Zinc's role in stress tolerance mechanisms is multidimensional. Zinc nutrition contributes to stress tolerance by triggering antioxidant machinery of the plants. Previously, Zn application triggered SOD and POD activities in *Triticum aestivum* under drought conditions (Yavas and Unay 2016). Likewise, Zn enhanced ascorbic acid and tocopherol production in green chili to scavenge free radical species (Manas et al. 2014). Zinc supplementation restored various types of lipids such as galactolipids, neutral lipids, total lipids, and phospholipids in Cd-affected tomato plants (Ammar et al. 2015). Zinc's role, as Cu-Zn SOD enzymes, is well established in combating drought stress in several plants like sugar beet (Hajheidari et al. 2005), periwinkle (Jaleel et al. 2007), and oilseed rape (Abedi and Pakniyat 2010). Similarly, the role of Cu-Zn SOD has been documented in lentil (Bandeoğlu et al. 2004), citrus (Gueta-Dahan et al. 1997), tobacco (Wang et al. 2003), and rice (Tanaka et al. 1999) to combat salt stress. Upregulation of two Cu-Zn SODs genes in various organs of tomato seedlings was also observed during plant development and stress induced by light (Perl-Treves and Galun 1991).

5.2.4 Chlorine

Essentiality of chlorine for various biological activities in plants is at par with other micronutrients. However, unlike other micronutrients, it is abundantly available in the soils and comparatively in greater amounts in plant tissues. Previous research has shown that average concentration of Cl in plants ranged from 2 to 20 mg/g on dry weight basis, while its average need is 0.2–0.4 mg/g for most of the plant species (Marschner 1995). Chlorine deficiency has been rarely reported in plants except in experimental setups to establish the role of Cl in biological systems. In a rare field study, Cl deficiency was proposed in coconut plant during dry season that led to disturbed stomatal functioning and changes in transpiration rates and reduced photosynthesis (Braconnier and Bonneau 1998). Chlorine maintains balance of charge in cells. The turgidity of guard cells in stomata is maintained by K influx from subsidiary cells and osmo-regulating property of chloride ion. Chlorine also plays role in photosynthesis as it binds covalently to Mn clusters in oxygen evolving complex in PSII (Rompel et al. 1997). Previously, chlorinated chlorophyll RC1 was suggested; however, later it was declared as experimental artifact (Senge et al. 1988).

Chlorine is an integral anion for more than 130 organic compounds in plants. A comprehensive detail of chlorine-containing compounds in higher plants has been given elsewhere (Engvild 1986). Chlorinated auxin such as chlorinated indole acetic acid (4-Cl-IAA) is found in the reproductive parts of the plants and stimulates synthesis of gibberellins and inhibition of ethylene action (Lam et al. 2015). Sesquiterpenoids are also Cl-containing compounds that have known role of disease resistance in plants (Weissenborn et al. 1995). Similarly, chlorinated phenols such as caffeoylquinic acids also called as chlorogenic acids, having antioxidant role, are accumulated in postharvest stress conditions (Jacobo-Velazquez et al. 2011).

5.2.5 Magnesium

Magnesium has several essential roles in plants. It is very crucial to photosynthesis as it is the central ion in both chlorophyll *a* and chlorophyll *b*. It is the key element to absorb sun's energy in the tetrapyrrol ring and helps fixing CO_2 in chloroplasts by modulating RuBP carboxylase activity. It is fundamental to numerous enzymes involved in synthesizing proteins, carbohydrates, lipids, and nucleic acids. Almost all enzymes in phosphorylation process and mitochondrial enzymes such as phosphatases, ATPases, and carboxylases have Mg as important component. Magnesium is implicated in sugar assimilation and starch synthesis by regulating nitrate reductase and glutamine synthetase. It activates amino acid synthesis, initiates and elongates polypeptide chain, and stabilizes structural and functional characteristics of ribosomes. Magnesium is also part of the metalloproteins involved in signal transduction.

Magnesium's deficiency can create stress conditions in plants. Previous research has shown that mulberry plants suffered Mg deficiency from stress (Tewari et al. 2006). Similarly, excessive ROS was generated in the photosynthetic EST in common bean and sugar beet deficient in Mg (Cakmak and Kirkby 2008). Similarly, in *Citrus sinensis*, proteomic analysis revealed that several proteins, related to photosynthesis and stress tolerance, were downregulated in leaves under Mg deficiency (Peng et al. 2015). Magnesium alleviated rhizotoxicity induced by aluminum stress in sensitive genotypes of soybean plants (Silva et al. 2001). Magnesium chelatase H subunit, an abscisic acid receptor and a protein of multifunction nature, is an important enzyme involved in chlorophyll biosynthesis and cell signaling. A study revealed that overexpression of Mg chelatase H subunit in *Arabidopsis thaliana* guard cells developed plant's tolerance to water deficiency-induced stress (Tsuzuki et al. 2013). In another study, leaf senescence in rice cultivars sensitive to salinity stress was enhanced due to reduced chlorophyll biosynthesis and decline in Mg concentration in leaves (Lutts et al. 1996).

5.2.6 Manganese

Manganese has several essential roles in plants such as maintaining chloroplast integrity, biosynthesis of fatty acids (FAs) and gibberellic acid (GA), and activation of RNA polymerase. However, contrary to other micronutrients, Mn mostly serves as activator or cofactor to enzymes. It is an integral part of metalloproteins and is required for the functioning of at least 35 different enzymes: either as activating agent or as metal cofactor. Three Mn-containing enzymes have been widely studied in plants, i.e., MnSOD, Mn-acid phosphatases, and Mn-enriched photosynthetic complex.

Manganese contributes to plant abiotic stress tolerance in several ways. It catalyzes MnSOD enzyme which quenches ROS in mitochondria. In a previous study, MnSOD overproduction protected transgenic tobacco plants from ozone-induced oxidative stress (Van Camp et al. 1994). Transgenic rice, transformed with MnSOD gene from pea, exhibited less cellular injury and enhanced tolerance to drought effects (Wang et al. 2005). Similarly, improved tolerance to cold stress was observed in maize chloroplasts transformed with tobacco MnSOD (Van Breusegem et al. 1999a). In winter wheat, foliar application of Mn along with Zn and B not only alleviated the harmful effects of water deficiency in late season but also enhanced agronomic traits of wheat (Karim et al. 2012). Likewise, transgenic *Arabidopsis thaliana* demonstrated resistance to salt stress by overexpressing MnSOD genes (Wang et al. 2004).

5.2.7 Molybdenum

Molybdenum is essential for several physiological functions of plants. Numerous biochemical functions in plants need Mo such as N assimilation, hormonal synthesis, etc. Molybdenum-containing enzymes are essential components of antioxidant system, for example, aldehyde oxidase, xanthine dehydrogenase, and nitrate reductase (Ventura et al. 2010; Brychkova et al. 2008; Yesbergenova et al. 2005). Members of aldehyde oxidase multigene family play role in biosynthesizing phytohormones such as abscisic acid and indole-3-acetic acid (IAA), by converting abscisic aldehyde and indoleacetoaldehyde to their related phytohormones (Leydecker et al. 1995; Koshiba et al. 1996; Sauer and Frebort 2003). IAA is placed in important plant hormone family known as auxins, which had abiotic stress role (Dunlap and Binzel 1996). Similarly, abscisic acid responds to different environmental stresses induced by salinity, drought, and temperature (Jiang and Zhang 2001; Walton and Yi 1995). Xanthine dehydrogenase is required in ureide biosynthesis and purine catabolism (Mendel and Bittner 2006; Mendel 2009; Brychkova et al. 2008). It triggers hypoxanthine hydroxylation to xanthine and uric acid. The latter is oxidized to ureides, enzymatically by uricase and nonenzymatically by ROS (Brychkova et al. 2008; Ventura et al. 2010; Santos et al. 1999). Nitrate reductase, another molybdenoenzyme, is vital for nitrogen metabolism in plants. It acts as catalyst in reducing nitrate ion to nitrite and then to ammonium (Bittner and Mendel 2010; Mendel 2009). In saline conditions, plants prefer nitrate as a N source, which increase plant resistance to salt stress (Cordovilla et al. 1996). Molybdenum application to wheatgrass also enhanced plant adaptation to salinity stress due to enhanced activities of molybdenum-containing enzymes, xanthine dehydrogenase, nitrate reductase, and aldehyde oxidase (Babenko et al. 2015).

5.2.8 Boron

Boron exhibits diverse structural, physiological, and biochemical functions in plants. It helps maintaining structural integrity and stability of cell walls and biomembranes. Growth and expansion of meristematic tissues and leaves are also B-mediated processes. Besides these, B plays role in cell division, ion absorption, water relations, metabolism of carbohydrates, hormones and IAA, and synthesis of nucleic acids, sugar transport, and protein synthesis. Earlier research has shown that B application enhances plant growth and development by maintaining the enzyme activation, pollen development, and charge balance in plant system (Ozturk et al. 2010).

Boron deficiency may cause slow or impaired vegetative and reproductive growth; however, biochemically, homeostasis of some important biomolecules and enzyme activities may be affected. Previously, B deficiency in tobacco seedlings caused decline in nitrate concentration and activity of nitrate reductase (Camacho-Cristóbal and González-Fontes 1999). Similarly, B deficiency significantly reduced stomatal conductance and photosynthetic rate in drought-stressed *Brassica rapa* plants (Hajiboland and Farhanghi 2011). Boron, in combination with Ca, improved seed germination and root elongation in salt-stressed *Pisum sativum* plants (Bonilla et al. 2004). Excess salts in root zone affect symbiotic relationship between plant roots and rhizobium. Boron, in combination with Ca, had demonstrated positive role in establishing rhizobial symbiosis in *Pisum sativum* under saline conditions (El-Hamdaoui et al. 2003). However, contrary to earlier findings, B co-application with NaCl caused more oxidative damage in *Lycopersicon esculentum* and *Cucumis sativus* leaves in the form of dry weight decline and increased membrane permeability (Alpaslan and Gunes 2001). This may be due to high dose of NaCl used in the experiment. In another study, deficiency of B activated antioxidant system in *Camellia sinensis* plants to alleviate stress induced by high light (Hajiboland et al. 2011).

5.2.9 Cobalt

Cobalt, a transition metal, performs several biological functions in plants like resistance to drought stress, regulating alkaloid accumulation, inhibition of ethylene biosynthesis, and synthesis of chlorophyll *b*. Cobalt is an integral part of vitamin B_{12} and helps in N fixation by root nodules. Moreover, Co is used in sterilization of fruits to increases their shelf life. Cobalt helps spectroscopic probing of metalloenzymes such as Zn enzymes to identify their structural characteristics (Dennis and Kolattukudy 1992).

To date, several enzymes containing Co have been identified in plants. Vitamin B_{12}-depedent enzymes contain axial Co group. Research has shown that Co is essential for the synthesis of hydrocarbons which are found under pathological conditions in plants. Co-porphyrin containing enzymes trigger decarbonylation of aldehydes which serve as precursors for hydrocarbon synthesis (Dennis and Kolattukudy 1992).

The direct role of Co, in abiotic stress tolerance, is mainly via modulation of antioxidants in plant systems. Suspension cell culture of *Crotalaria cobalticola*, a Co-hyperaccumulator plant, demonstrated increased citric acid and free cysteine contents, suggesting the later involvement in Co complexation in the plant under study (Oven et al. 2002). Indirectly, Co may add to abiotic stress tolerance by inhibiting toxicants or ROS generators in plants. It is suggested that Co may cause Fe deficiency in some plants and may inhibit cadmium (Cd) uptake. Under water stress, Co is supposed to inhibit biosynthesis of IAA-induced ethylene formation in various plant species such as wheat, kidney beans, ferns, etc. In another study, excess Co caused oxidative stress in *Phaseolus aureus*; however, H_2O_2 generation and lipid peroxidation were reduced due to enhanced activities of SOD and APX (Tewari et al. 2002).

5.2.10 Selenium

Selenium is a nonessential but beneficial trace element for higher plants. Generally, Se concentration in soils is very low; however, in seleniferous soils, it builds up to 100 mg kg^{-1} (Pilon-Smits 2015). Selenium is analogous to sulfur (S) having similar valencies on its ionic forms and follows S assimilation pathways to assimilate as selenocysteine (SeCys) which is easily incorporated into proteins, selenomethionine (SeMet), and other S compounds. Basically, Se, as SeCys, is an active part of selenoproteins like glutathione peroxidase and thioredoxin reductase which have ROS scavenging abilities.

Selenium's role in combating abiotic stresses caused by UV light, drought, heavy metals, cold, and salts is well documented in earlier literature. Previously, it helped promoting growth of rye grass, delaying drought, and inducing tolerance to UV-induced stress (Cartes et al. 2010; Hasanuzzaman and Fujita 2011; Hasanuzzaman et al. 2014). Similarly, under drought stress, Se pretreatment of rapeseed enhanced antioxidant enzyme activities and increased concentration of AsA and glutathione (Hasanuzzaman and Fujita 2011). In another study, Se improved physiological growth of wheat seedlings under drought stress in the form of increased biomass accumulation and root elongation and elevated CAT and POD activities (Yao et al. 2009). Selenium treatment also protected sunflower seedlings from cadmium-induced oxidative stress by boosting CAT, APX, and GR activities (Saidi et al. 2014). In another hydroponic experiment, exogenously applied Se mitigated Cd stress in rice by inhibiting Cd uptake, maintaining nutrient balance, and modulating ATPase activities in roots and leaves (Lin et al. 2012). In another study, exogenous Se application increased plant biomass and chlorophyll concentration in wheat seedlings along with elevated contents of anthocyanins, phenols, and flavonoids under cold stress (Chu et al. 2010).

5.3 Conclusion

Trace elements are vital components of cell structures and play roles in plant metabolisms. However, adverse conditions like drought, salinity, toxic compounds, abnormal temperatures, and excess light may disturb normal cellular activities and plant growth. Trace elements help plants to cope with these abiotic stresses by several mechanisms including activation of antioxidant defense system, regulation of metabolic activities, synthesis of biomolecules, and maintenance of ionic homeostasis. Thus, adequate supply of trace elements, as per plant requirement, can promote plant growth both under normal and abiotic-stressed conditions.

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Chapter 6
Biomolecular Functions of Micronutrients Toward Abiotic Stress Tolerance in Plants

Shyam N. Pandey

Abstract Many of the world's cultivated areas are facing various abiotic stresses such as drought, salinity, temperature extremes, and nutrient abnormalities. For the maintenance of crop productivity, improvement of the micronutrient status in plants under abiotic stress is very important. In most cases of abiotic stress, plants experience either poor or excessive availability of micronutrients, which alters their biochemical composition and minimizes growth and yield. Micronutrient availability greatly affects the ability of plants to adapt to unfavorable conditions. Essential micronutrients, such as zinc (Zn), copper (Cu), manganese (Mn), boron (B), iron (Fe), molybdenum (Mo), chloride (Cl), nickel (Ni), and cobalt (Co), have direct roles in plant metabolism. Most of these nutrients have two or more oxidation states, and therefore participate in oxidation–reduction reactions through electron transport. These elements form metalloenzymes, function as catalysts, and are vital in osmoregulation and protection against abiotic stress in plants. Micronutrients protect plants by functioning as constituents and activators of several enzymes in their defense system [such as catalase, ascarbate peroxidase, superoxide dismutase (Zn-SOD, Cu-Zn SOD, Fe-SOD, Mn-SOD)] that are involved in the detoxification of highly reactive oxygen species (ROS) produced during abiotic stress. In the present study, the role of micronutrients in the growth and metabolism of plants, as well as their support to the plants for protection, adaptation, and tolerance against abiotic stress through supporting biochemical activities, is emphasized.

Keywords Micronutrients · Abiotic stress · Biochemical constituents · Reactive oxygen species

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6.1 Introduction

Our increasing population and shrinking agricultural land areas impose tremendous pressure on plant production throughout the world. The economy of almost all countries, directly and indirectly, is dependent on plant yield. But a huge area of the Earth's land mass is facing various adverse environmental problems such as salinity, drought, heavy metal pollution, and water surpluses or deficits (Singh et al. 2015). These abiotic stress conditions cause great depletion in plant productivity (Verma et al. 2014). In recent years, climatic changes have continuously placed various stresses on plants and the survival of other living organisms (Romero et al. 2017). Every species must be in harmony between its internal and external constituents and the environment in which they live (Ma et al. 2017); when they are not adapted to the changing environment, they are expelled. Abiotic stresses are caused by changes in environmental components such as gases (ozone, CO_2, nitrogen oxide), water, temperature, minerals, and climatic variables. For plant growth and food production, nutritional balance in the growth medium is very important, as well as normal environmental conditions. The mineral status of plants affects their ability to adapt under the influence of abiotic stresses (Singh et al. 2015). Under the influence of abiotic stresses such as salinity, drought, or high temperature, plants require additional micronutrients (Pandey 2006; Pandey et al. 2009; Kannaujiya and Pandey 2013). The important micronutrients such as zinc (Zn), manganese (Mn), copper (Cu), iron (Fe), molybdenum (Mo), boron (B), and chloride (Cl) have been studied for their part in the survival of plant life during abiotic stresses (Alscher et al. 2002; Asad et al. 2003; O'Neill et al. 2004; Beak et al. 2015). When plants that are growing under abiotic stress conditions receive more light more than their requirements for photosynthesis during electron transport and the fixation of carbon dioxide, reactive oxygen species (ROS) are formed. The excess accumulation of radiant energy and photoreductants in the chloroplast activates molecular oxygen (O_2) and highly reactive oxygen species (Gibbs and Greenway 2003). The one-step reaction of oxygen and hydrogen peroxide generates superoxide ions ($O_2^{\bullet-}$); such superoxide ions when dismutated by the superoxide dismutases generate two reactive oxygen species that lead to oxidation of lipid membranes and damage of cellular constituents. $O_2^{\bullet-}$ and H_2O_2 react with each other, producing more toxic hydroxyl radicals (Haber–Weiss reaction). This reaction is catalyzed by ionic iron (Sharma 2006). Free ferrous ion reacts with H_2O_2 to produce hydroxyl radicals (Fenton reaction):

$$Fe^{2+} + H_2O_2 \rightarrow Fe^{3+} + OH^{\cdot} + OH^{-}$$

The ferric ions produced in this reaction, on reacting with superoxide ions, are cycled back to ferrous ions. Thus, a small quantity of free inorganic ion accelerates the reaction, producing highly toxic hydroxyl radicals that damage the cell. Although such micronutrients aid in the production of superoxide radicals by functioning as a part of the enzymes of the defense system (Beak et al. 2015), they are important in neutralizing $O_2^{\bullet-}$ by dismutating the radicals to H_2O_2. During abiotic stress, the generation of highly reactive oxygen species damages membrane lipids, protein, and DNA, inducing mutations (Ditch and Paull 2012). Some important enzymes that contain micronutrients as constituents, such as catalase (CAT), ascorbate peroxidase (APX), and superoxide dismutase (Fe-SOD, Mn-SOD, Cu-Zn SOD), act as a defense against oxidative stress.

6.2 Micronutrients

Based on quantitative requirements for functional activities of plants, micronutrients are required in smaller quantities (<1 ppm). Many times more macronutrients are required by plants (>1 ppm). Micronutrients such as Mn, Cu, Zn, Fe, Mo, B, Cl, and Ni have direct roles in plant metabolism (Pandey 2014). Cobalt and nickel have been added recently to the list of essential nutrients. The essential role of cobalt in nitrogen fixation in leguminous plants (Ahmed and Evans 1960; Dilworth et al. 1979) and non-leguminous plants (Hewitt and Bond 1966; Johnson et al. 1996) has been reported. Its essential function for rhizobial growth (Cowles et al. 1969), as a cofactor of cobalamine (vitamin B_6), which functions as a coenzyme in nitrogen fixation and nodule growth, has been identified (Dilworth et al. 1979; Jordan and Reichard 1998; Pandey and Verma 2010). Gerendas et al. (1999) claimed nickel as an essential nutrient, present in substantial concentrations in the xylem and phloem sap as chelate (Ni-citrate) and a cofactor of jack bean urease (Gerendas and Sattelmacher 1997).

In the periodic table, Fe, Mn, Cu, Zn, Ni, and Co are in the cationic group in periods 4 and 5 (Mo). Most of the micronutrients, except B and Cl, are transitional elements. These micronutrients create a stable complex with organic ligands. They form metalloenzymes that function as catalysts and form a complex with proteins. Excepting Ni and Zn, they have two or more oxidation states, and therefore participate in oxidation–reduction reactions through electron transport (Sharma 2006).

6.3 Functions of Micronutrients

Micronutrients are important constituents of organic structure activators of enzymes and electron carriers and are present in the osmoregulation process (Bughio et al. 2002; Upadhyay et al. 2013): they are involved in cellular metabolism, reproduction processes, and protection against abiotic and biotic stress (Asad et al. 2003). The essential micronutrients support plant growth and development under abiotic stress conditions by their direct role in the growth, metabolism, and biosynthesis of molecules in the plant cells (Pandey 2014).

6.3.1 *Constituents in Organic Structures*

Some micronutrients such as boron and zinc are constituents of the plant cell wall (O'Neill et al. 2004), maintaining the function and structural integrity of the plasma membrane (Yu et al. 2003). Membrane structure is stabilized by the binding of boron to polyhydroxy groups of the membrane constituents (Brown et al. 2002). Zinc has a role in plasma membrane permeability (Cakmak and Marschner 1988) and in the protection of plant cells from damage by reactive oxygen species (Cakmak 2000; Apel and Hirt 2004; Pandey 2014).

6.3.2 *Enzyme Action*

The main function of micronutrients is catalytic, regulating enzyme-catalyzed reactions. Also, micronutrients are constituents of several enzymes (Alscher et al. 2002). The micronutrients zinc, copper, molybdenum, manganese, and iron are constituents of oxidoreductases. The metal–enzyme complexes are involved in various functions such as photosynthesis, mineral metabolism, respiration, the biosynthetic pathway, and the abiotic stress defense mechanism (Slooten et al. 1995).

The activities of most hydrolyases are concerned with zinc and manganese; lyase activity is catalyzed by iron, zinc, and manganese (Sharma 2006). Micronutrients perform catalytic functions by their specificity to binding proteins (e.g., copper oxidases and heme-enzymes), by causing the net charges on the protein, affecting enzyme–substrate complexes (for example, the ratio of magnesium and zinc alters the optima of phosphatase activity), by forming a bridge between enzyme and substrate, and form as a complex and act as activators of enzymes (e.g., manganese-activated decarboxylases and hydrolyases). Micronutrients also cause allosteric effects on enzyme activity as they bind at sites other than the enzyme active site (Sharma 2006).

6.3.3 *Charge Carriers*

Micronutrients are cofactors of enzymes; they catalyze redox reactions. Metals binding with proteins behave as electron carriers. Therefore, they are important in electron transport chains in cellular metabolism, facilitating the transfer of electrons from one molecule to another. In photosystem II (PS II), manganese induces charge accumulation to produce the reducing power required for photolysis of water to initiate the reactions of photosynthesis.

The variable oxidation states of molybdenum catalyze the enzymatic reduction of the N=N bond in N_2 to NH_4 (Sharma 2006). At the inner mitochondrial membrane, the electron transport protein contains copper and zinc as cofactors. The responsible enzyme catalyzes reduction of NAD^+ to NADH in the mitochondrial matrix. Cu and Fe are two important electron carriers in the electron transport system. At the start of photosynthesis in PS II, manganese is important in the oxidation of water as Fe and Cu participate in electron transport through PS II and PS I and in coordinating the flow of electrons from PS II to PS I (Ono and Onone 1991).

6.3.4 Osmoregulation

Soil–plant relationships usually exist depending only on the water status in both. Micronutrients influence these plant–water relationships. Chlorine has a very important role in osmoregulation, maintaining the osmotic potential of the cell and turgor-dependent extension growth of cells. Chlorine and potassium induce turgor changes to regulate the stomatal opening, which responds to the fluxes of Cl^- and K^+ ions across the leaf guard cell plasma membrane (Alaya and Palmgren 2001). Under salt stress conditions, chlorine functions in the osmoregulatory process (Henstein and Felle 2002).

6.3.5 Secondary Metabolism

Growth hormones and micronutrients are involved in many biosynthetic pathways. Many enzymes catalyze reactions in biosynthetic pathways, and secondary metabolism contains micronutrients as activators. The shikimate pathway produces precursors important in the synthesis of aromatic amino acids. In the shikimate pathway, the initial reaction involves the condensation of phosphoenolpyruvate and erythrose-4-phosphate to the synthesis of 3-deoxy-D-arabinoheptulosonolate-7-phosphate (DAHP); the enzyme DAHP synthase acts as catalyst in initiation of the shikimate pathway activated by Mn (Herrmann and Weaver 1999). The enzymes involved in synthesis of lignin contain Fe and Zn. Plant growth hormone gibberellins are recognized as signaling molecules in plants (Sun and Gubler 2004). Synthesis of gibberellins involves several enzymes activated by a number of micronutrients. Kaurene synthase catalyzes the *ent*-kaurene precursor of synthesis of gibberellins activated by Mn^{2+}, Co^{2+}, or Mg^{2+} (Chapple 1998; Schomburg et al. 2002). The enzymes that are involved contain Fe as cofactor. A non-heme enzyme, lipoxygenase, contains iron (Feussner and Wasternack 2002). The enzymes involved in the biosynthesis of ethylene and abscisic acid have micronutrient cofactors (Romao et al. 1995; Prescott and John 1996). The synthesis of anthocyanin and flavones involves catalysis by cytochrome P_{450} heme monooxygenase (Chapple 1998).

6.3.6 Protective Role

Micronutrients detoxify the activity of ROS, the reactive oxygen species generated by abiotic stress or for other reasons in the cell (Romero et al. 2017), induce oxidative stress, and have a role in signal transduction (Apel and Hirt 2004; Ma et al. 2017). The enzyme proteins with micronutrient cofactors participate in the defense antioxidant system, with a significant role in protection against damage by the generation of ROS (Ma et al. 2017). The enzyme SOD, such as Fe-SOD, Cu-Zn-SOD, and Mn-SOD, have micronutrient cofactors that provide defense against highly reactive oxygen species (Alscher et al. 2002). In the chloroplast, the activity of Fe-SOD and Cu-Zn SOD and in mitochondria the activity of Mn-SOD are more prominent. Therefore, the superoxide ions are rapidly converted to H_2O_2 in a high concentration in the cytosol. Elevated H_2O_2 concentrations in cell are highly toxic, prevented by conversion to water molecules. Such detoxification reactions are catalyzed by APX and CAT. Ascorbate as a specific electron donor reduces H_2O_2 to water with the production of monodehydroascorbate (Asada 1997). The ascorbate–glutathione cycle and APX activity function as potent scavengers of hydrogen peroxide, which is highly concentrated in peroxisomes, and carry out the breakdown of hydrogen peroxide. The formation of glyoxlate from glycolate also contributes H_2O_2. Antioxidant enzymes containing the micronutrients Fe, Cu, Mn, or Zn as cofactors include SOD, APX, and CAT. These enzymes are significant in the detoxification of ROS (Jaleel et al. 2009).

When abiotic stress conditions lead to micronutrient deficiency, the metal cofactors are less available to antioxidant enzymes, which weakens the defense system in plants (Pandey 2014). The role of micronutrient Zn in the defense system of plants against oxidative stress has been proved (Cakmak 2000; Beak et al. 2015). The micronutrient iron is a cofactor of chlorine monooxygenase in gylcine betaine-accumulating plants. Glycine betain acts as an osmoprotectant; the first step of its biosynthesis is catalyzed by chlorine monooxygenase (Sharma 2006). During abiotic stresses such as high temperature and high salinity, glycine betaine contains Fe as a cofactor stabilizing the quaternary structure of proteins and maintaining the structural integrity of cellular membranes (Gorham 1995). Micronutrients also provide protection to the plants from pathogens (Huber and Graham 1999). Some micronutrients such as Zn, B, and Mn are involved in the synthetic process of lignins and suberins or produced antioxidants, which strengthen the cell walls for protection against pathogens (Mehdy 1994; Orozeo-Cardinas et al. 2001; Cao et al. 2016). The homologue genes *AtTZF1*, *AtTZF2*, and *AtTZF3* have been identified in evolutionarily distant plant species regulated by salt stress (D'Orso et al. 2015).

6.3.6.1 Iron

Iron exists in two oxidative states (Fe^{2+} and Fe^{3+}), and participates in oxidation–reduction reactions and in electron transport. Iron forms the prosthetic group of several enzymes such as catalase, peroxidases, and cytochrome *c* oxidase. Iron is involved in detoxification of ROS generated during abiotic stress conditions. Iron homeostasis is significant to sustain metabolism during abiotic stresses. During oxidative stress, iron enhances the tolerance of plants through formation of the antioxidant system. Overexpression of choline monooxygenase and a cytochrome P_{450} monooxygenase helps establish osmoprotection against high temperatures and salt stress. Reduction of Fe^{3+} and Fe^{2+} at the plasmalemma promotes various mechanisms for the protection of cell metabolism during abiotic stresses (Rabotti and Zocchi 1994). A variety of non-heme iron enzymes contain Fe cofactor from an iron sulfur cluster (Johnson et al. 2005).

Several transporter genes for iron transport have been identified from IRT1 (iron regulator transporter 1) of the ZIP family in *Arabidopsis* (Eide et al. 1996). It has been reported that the IRTI mutant line needs a high Fe supply from the soil to the plants (Vert et al. 2002). The gene IRT2 in *Arabidopsis* responsible for Fe transport is activated during Fe deficiency (Grotz et al. 1998). Two environmental DNAs (eDNAs), Le IRT1 and Le IRT2, are expressed in the Fe-deficient roots (Eckhardt et al. 2001). Nramp family transporters (Nramps 1, 3, 4) are involved in uptake and vascular transport of Fe and other co-substances (Cd and Mn) in plants (Curic et al. 2000; Thomine et al. 2003). In the pea, the Fe^{3+} chelate reductase gene FRO1 exhibits its expression in response to iron deficiency (Waters et al. 2002).

The peroxidase enzymes, encoded by a large multigene family, catalyze the dismutation of H_2O_2 to water. In abiotic stress, iron is protective for plants against reactive oxygen species. Although iron is involved in the generation of ROS (Becana et al. 1998), as a constituent of enzymes it also aids in the detoxification of O_2 by dismutation to H_2O_2. The heme enzymes CAT and APX act as scavengers of H_2O_2 in the cell. Iron is a cofactor of Fdx-choline monooxygenase, which is involved in the synthesis of glycine betaine, an osmoprotectant of plants during high temperature and high salinity conditions (Gorham 1995).

6.3.6.2 Manganese

Manganese exists in several oxidation states in plants: Mn^{2+}, Mn^{3+}, Mn^{4+}, and Mn^{5+}. The most dominant form is manganous, Mn^{2+}. The manganese–enzyme complex catalyzes cellular metabolism and is also involved in carbon dioxide fixation in crassulacean acid metabolism or CAM photosynthesis and C_4 plants. It also detoxifies oxygen free radicals. Manganese is a constituent of more than 30 enzymes (Burnell 1988). The specific role of Mn in some enzymes in plants is neutralizing the adverse effects of abiotic stress as Mn superoxide dismutase (Mn-SOD), phosphoenol pyruvate carboxy kinase (PEPCK), NAD^+-malic enzyme, allantoate amidohydrolase, isocitrate dehydrogenase (IDH), phosphoenol pyruvate carboxylase (PEP-case), enolase, etc.

Mn-SOD is a Mn^{3+}-containing dimeric protein binding to substrate ($O^-{}_2$), and manganese undergoes oxidation–reduction ($Mn^{2+} \leftrightarrow Mn^{3+}$). This metallic protein functions in the antioxidant defense system of mitochondria in cells, forming a site for the generation of ROS. Manganese as a constituent of PEPCK, and NAD^+-malic dehydrogenase assists the fast growth of plants when grown in drought stress conditions, particularly C_4 plants (Chen et al. 2002). The PEPase activated by Mn^{2+} has a key biosynthetic role in plants, involved in the biosynthesis of the amino acids aspartate and glutamate. It also functions as a CO_2-concentrating mechanism in C_4 plants under high drought stress conditions. The function of Mn in the oxidation of water in PS II is well established (Ono and Onone 1991; Hoganson and Bobcock 1997). Manganese is an activator of arginase, involved in the synthesis of polyamines in plant growth and development (Sharma 2006), and in detoxification of active oxygen species formed during various abiotic stress conditions.

Under salt stress conditions, Mn deficiency is expressed by plants because of its poor uptake (Sharma 2006). In plants, Mn deficiency causes changes in enzyme activity. Mitochondrial Mn-SOD is a constituent of the antioxidant system, in which Mn provides protection against oxidative damage (Slooten et al. 1995). The enzyme Mn-SOD is also suggested to contribute to drought tolerance in plants. An increase in Mn-SOD expression in plants on the induction of drought-like conditions and a decrease in its expression on rehydration of the plants have been described (Wu et al. 1999, 2002).

6.3.6.3 Zinc

Zinc has only one oxidation state (Zn^{2+}), and therefore it is not involved in oxidoreductase activity. It has a functional and structural role in plants. Zinc ions bind to nitrogen- or sulfur-containing ligands through ionic bonds in tetrahedral geometry. It is a cofactor of more than 300 enzymes (Sharma 2006). In heavy metals stress conditions, at its excess level peptides form metalloproteins, phytochelatins and metallothioneins, which contribute tolerance against the excess accumulation of heavy metals in the plant tissues. Zinc is important in the prevention of water stress and also protects plant cells against damage by reactive oxygen species. Under salt stress conditions (saline, sodic, or calcareous soils), plants exhibit Mn deficiency (Pandey 2014; Pandey et al. 2009). Several transporters belonging to the ZIP (ZRT-IRT-like proteins) and CDF (cation diffusion facilitator) families are involved in transport of zinc (Guerinot 2000). Zinc transporter genes ZIP1, 2, 3, and 4 have been isolated (Guerinot 2000; Moreau et al. 2002) from *Arabidopsis*. Another gene responsible for zinc transport, ZNT1, has been cloned from the high Zn or Cd accumulator plant *Thlaspi caerulescens* (Assuncao et al. 2001). Under excess Zn in growth medium, a cation diffusion facilitator family transporter, ZAT, isolated in *Arabidopsis* transport of Zn (Van der Zaal et al. 1999), leads to increased accumulation of Zn. ZAT transport of Zn causes vascular/vacuolar sequestration of Zn to provide tolerance against excess Zn stress and contributes homeostasis (Van der Zaal et al. 1999). Zinc inhibits the production of ROS through inhibition of NADPH oxidase activity on the plasma membrane (Cakmak and Marschner 1988). Under salt stress conditions (saline, alkali, or calcareous soils), Zn deficiency induces the activation of RNAase (Bisht et al. 2002). In areas of high temperature and low precipitation, soils with high pH (>7.5) are deficient in Zn (Pandey 2014). Plants grown in such conditions show a decreased rate of photosynthesis (Sharma et al. 1994) and changes in chloroplast structure and CO_2 fixation (Shrotri et al. 1978).

A decrease in photosynthesis under conditions of Zn deficiency caused by decreased activity of carbonic anhydrase and disorganization of chloroplast thylakoids has been demonstrated (Henriques 2001). Some important enzymes containing Zn as an constituent are carbonic anhydrase (CA), Zn-SOD, alcohol dehydrogenase (contains two Zn atoms per molecule), carboxypeptidases, and DNA-dependent polymerases. Carbonic anhydrase catalyzes the reversible conversion of CO_2 to bicarbonate, a substrate in the photosynthesis of C_4 plants for carboxylation reaction catalyzed by phosphoenolpyruvate carboxylase. In C_3 plants, CA is localized in the chloroplast of mesophyll cells. Zn-superoxide dismutase is involved in the defense system against ROS formed by abiotic stress. Anaerobic stress conditions such as flooding enable the plant root tissues to temporarily meet their energy need from ethanolic fermentation (Gibbs and Greenwary 2003; Ravichandran and Pathmanabhan 2004). Ethanol is formed during glycolysis with catalytic activity of alcohol dehydrogenase. A Zn-metallo-enzyme carboxypeptidase catalyzes the hydrolysis of the peptide bond at the C-terminal end by activating a water molecule. The activity of several enzymes is inhibited during abiotic stresses, such as excess basic salts that cause Zn deficiency.

A plasma membrane H^+-ATPase of maize roots uses Zn as the substrate and functions as Zn-ATPase (Sharma 2006). Zinc is also a constituent of some regulatory proteins that control gene expression. The zinc finger forms a structural motif of the DNA-binding region of the transcriptional regulatory proteins (Berg and Shi 1996). Abiotic stresses such as salt and high temperature in arid and semi-arid regions cause Zn deficiency, which causes damage to the structural integrity of biomolecules responsible for the leakage of K^+, amino acids, sugars, and phenolics from the cell (Lindsay et al. 1989). Zinc protects the –SH groups of plasma membrane proteins from oxidative damage (Beak et al. 2015). Production of ROS under abiotic stress conditions that damage the plant cells can be prevented by Zn-metalloprotein (Cakmak 2000). Zinc prevents the production of ROS either by their rapid detoxification, or by inhibition of the activity of membrane-bound NADPH oxidase, which catalyzes the production of superoxide ions. A high accumulation of superoxide ions ($O_2^{\bullet-}$) leads to the formation of hydroxyl ($^{\bullet}OH^{\cdot}$) radicals (Haber–Weiss reaction), which are many times more reactive then $O_2^{\bullet-}$ and may cause more severe damage to the cellular membrane.

6.3.6.4 Copper

Copper is present in organic complexes in soils. Its divalent form (Cu^{2+}) is adsorbed to soil organic matter, carbonates, hydrous oxides of Fe, Al, and Mn, and forms organic complexes with sulfur, oxygen, and nitrogen atoms. The formation of Cu–organic complexes causes copper deficiency in the soil. In the alkaline pH range, copper availability also decreases (Pandey 2006). Because of its reversible change in oxidation state, copper does not function in oxidation–reduction reactions. Copper as a constituent of many enzymes functions as an electron carrier catalyzing oxidation–reduction processes in cellular metabolism (Sharma 2006).

Protein plastocyanin and cytochrome *c* oxidase containing Cu function as electron carriers in the cell. Copper is also useful in detoxification of superoxide radicals, pollen fertility, and lignification of plant cell walls. Recently, the five putative copper transporters *COPT1, COPT2, COPT3, COPT4*, and *COPT5* have been identified in *Arabidopsis* (Sancenon et al. 2003). Copper transport takes place as a complex with the amino acids histidine, asparagine, and glutamine acid observed in soybean and tomato (White et al. 1981; Loneragen 1981). Metallochaperones are intracellular metal transport proteins that transport copper ions from the cytoplasm to the functional sites (O'Halloran and Culotta 2000) or functional proteins such as Cu-Zn SOD (Huffman and O'Halloran 2001). A dimeric blue copper protein ascorbate oxidase catalyzes the dehydrogenation of ascorbate to dehydroascorbate, coupled to the four-electron reduction of molecular oxygen to water. In this enzyme, eight copper ions (Cu^{2+}) are bound per mole enzyme proteins of wide occurrence in the cytoplasm of plant cells and cell walls. Catechol oxidase contains four copper ions per mole; it catalyzes the oxidation of *o*- or *p*-diphenols to quinines coupled to the reduction of molecular oxygen to water. Such enzymes are involved in the biosynthesis of lignin and synthesis of plastoquinone involved in PS II electron transport (Ayala et al. 1992). The superoxide dismutase (Cu-Zn SOD) carries out the disproportionation of reactive oxygen species to H_2O_2 and O_2. The reactive oxygen species forms mostly in response to abiotic stresses. Cu-Zn SOD detoxifies the damage of ROS.

Similar to Cu-Zn SOD, APX bound to the thylakoids in vicinity of the PS II (Miyake et al. 1993) catalyzes the ascorbate base reduction of H_2O_2 to water. Cytochrome *c* oxidase contains three copper ions and two heme molecules as cofactors. It catalyzes the reduction of molecular oxygen to water in the terminal step of mitochondrial electron transport. Copper is also present as a cofactor in nitrite and nitrous oxide reductases of denitrifying bacteria. As a constituent of plastocyanin, copper links PS II and PS I and their cooperative functioning in noncyclic transport of electrons from water to NADP. Copper bound in some polypeptides maintains the lipid environment favoring the movement of plastoquinone molecules during PS II electron transport (Baron et al. 1995; Maksymiec 1997).

During abiotic stresses such as those from saline, alkaline, or calcareous soil, coarse-textured soil in arid and semi-arid regions mostly shows copper deficiency in plants (Pandey 2006). Copper deficiency in the soil causes reduced chlorophyll content and photosynthetic rate in plants (Pandey et al. 2002) and failure in the plant defense system (Sancenon et al. 2003), because the supply of copper affects the maturation of seeds (Nautiyal and Chatterjee 1999), increases the activity of invertase and amylase, and decreases the seed reserves of starch and proteins (Nautiyal et al. 1999).

6.3.6.5 Molybdenum

Molybdenum occurs in soil predominantly as molybdate anion (MoO_4^{2-}), which is stable at pH 4. Polymerization occurs above and below this pH. Molybdenum exists in several oxidation states: Mo(II), Mo(III), Mo(IV), Mo(V), Mo(VI). The most stable oxidation state is the hexavalent form. Molybdenum has a high affinity for oxygen- and sulfur-containing groups. It is the cofactor of several enzymes either singly or in combination with other elements such as Fe, Cu, and S (Hille 1996; Sigel and Sigel 2002). Molybdenum is an essential metal for the process of nitrogen fixation by bacteria. The uptake of Mo involves the same transporter gene as is involved in the transport of phosphate (Heunwinkle et al. 1992; Marschner 1995). Llamas et al. (2000) suggested the involvement of more than one transporter in Mo uptake in mutant analysis of *Chlamydomonas*. Molybdenum is the cofactor of several enzymes such as oxidase-catalyzed redox reactions (Stiefel 1996). The molybdenum-containing enzymes nitrate reductase and xanthine oxidase catalyze the reactions of nitrogen and its compounds, and aldehyde oxidase catalyzes the reactions of the biosynthetic pathway of abscisic acid (Taylor 1991) and auxins (Koshiba et al. 1996). Several enzymes containing Mo as cofactor are also associated with additional cofactors such as Fe-S, iron, and flavin (Mendel and Hansch 2002). Nitrate reductase catalyzes electron transfer from NAD(P)H to molecular oxygen, producing superoxide ions and to nitrite, producing nitric oxide (Kaiser et al. 2002; Rockel et al. 2002).

6.3.6.6 Boron

In soil solution, boron is present in several forms: BO_2^-, B_4O_7, BO_3, $H_2BO_3^-$, and $B(OH_4)$. Boron exists in three valency states and has a strong affinity for oxygen. In plants, boric acid forms complexes with hydroxyl radicals of compounds (Loomis and Durst 1991). The role of B in cross-linking of cell wall polysaccharides has been observed by O’Neill et al. (2004). The uptake of B from soil is both active and passive (Pfeffer et al. 1999; Dordas and Brown 2000). If boron is adequately available in soil, its uptake is passive, but when boron is in short supply, it is taken up by an active metabolic process (Pfeffer et al. 1999; Dannel et al. 2000). Boron forms diester bonds with diol groups of polysaccharides for cell wall structures (Hu et al. 1997). Borate provides tensile strength to cell walls (O’Neill et al. 2001). Boron deficiency affects the accumulation of cytoskeletal protein in maize (Yu et al. 2003). Boric acid prevents the oxidation of phenols by forming boron–phenol complexes (Cakmak et al. 1995). Cara et al. (2002) suggest that boron ATPase and ferric chelate reductase function in the plasma membrane in severe boron deficiency (Brown et al. 1999). Boron deficiency decreases photosynthetic oxygen evolution (Kastori et al. 1995) and decreases the rate of PS II electron from oxidative damage caused to the thylakoid membranes (El-Shintinawy 1991). Boron is also involved in carbohydrate metabolism (Sharma 2006). Inhibition of nitrate reductase activity and accumulation of nitrate caused by boron deficiency were reported by Camacho-Christobal and Gonzalez-Fontes (1993). Boron deficiency occurs during abiotic stresses such as high salt, high temperature, and low water availability, which decrease nucleic acid concentration and the enzymes involved in nucleic acid metabolism (Agarwala et al. 1991).

Boron is involved in the synthesis of polyphenols, lignin, flavonoids, and alkaloids (Dixit et al. 2002). Under oxidative stress, boron deprivation in tobacco cells causes overexpression of early salicylate-inducible glucosyltransferase and glutathione-*S*-transferase genes (Kobayashi et al. 2004) for a defense system against oxidation stress from boron.

6.3.6.7 Chlorine

Chlorine has a single stable oxidation state (Cl^-). It is involved in more than 130 chlorine-containing organic compounds in plants. Chlorine is a component of the manganese cluster of PS II that catalyzes the oxidation of water. It is also involved in the activity of auxin (Sharma 2006). In living cells, it maintains turgor and osmoregulation; chlorine is also involved in the regulatory mechanism of enzyme action and the functioning of the stomata (Xu et al. 2000). In soil, chlorine is present as chlorine (Cl^-) ions and occurs naturally as organochlorine. Compound salts of chlorine are highly soluble and mobile in the rhizosphere (White and Broadley 2001). Environmental contaminants from various sources also contribute Cl^- in soil and plants (Pandey 2014). The transport of Cl^- across plasma membranes involves an active component (Felle 1994), proton pump (H^+ATPase), and a passive component (facilitates diffusion) mediated through anion channels (Skerrett and Tyerman 1994). Under high concentration of Cl^- (high saline), passive transport dominates, and at its low concentration active transport proceeds (White and Broadley 2001). In a study on transgenic *Arabidopsis* by Lorenzen et al. (2004), under saline conditions chloride ion influx is passive through symport (anion transport coupled with the transport of cation) protein channel. The transport of chloride from root to shoot takes place through the xylem, which is influenced by the rate of shoot growth and transpiration (Storey 1995; Moya et al. 1999). Under salt stress conditions, chloride is phloem mobile (Lohaus et al. 2000). In the Mn-containing oxygen condition complex of PSII, chlorine is a constituent (Hoganson and Babcock 1997). Thus, deficiency of Cl decrease oxygen evolution of photosynthesis and also reduces cell division and plant growth as well as affecting stomatal functioning and carbon dioxide exchange (Sharma 2006).

During abiotic stress, Cl is important in the osmoregulatory process in plants. In plant roots, Cl functions as an osmotically active solute (Flowers 1988). Chloride accumulates in the extension zone of the growing root and the shoot apex at higher concentrations, promoting the turgor-induced extension growth of root and shoot apices. Chlorine does not act directly as a catalyst. It stimulates the enzyme asparagine synthetase, which catalyzes the process of asparagine synthesis involving glutamate. In the conversion of aspartate to asparagine, the process is also catalyzed by asparagine synthetase. Asparagine has a role in the storage of nitrogen and its transport from source to sink; it is found in the phloem sap of several legumes. The deficiency of Cl^- restricts the area of the young leaves by reduction in cell division rate and decrease in the osmoticum.

Under abiotic stress conditions such as hot sunny days, excess salt in growth medium, etc., the wilting of leaf margins is very prominent (Sharma 2006), possibly because of the impairment of osmoregulation.

6.4 Conclusion

Plants are continuously facing changes in environmental constituents that cause abiotic and biotic stresses. Also, plants growing in the large arable areas of the world are affected by imbalances in micronutrients. The essential micronutrients such as zinc, copper, manganese, iron, boron, molybdenum, and chlorine, required in smaller quantities, have a vital role in plant growth and in protection against various stresses. During abiotic stresses such as drought, salinity, deficiencies and toxicities of nutrients, and extremes of temperature, the status of micronutrients in soil and plants is important to the functions of osmoprotection, enzyme activity, biosynthesis of cellular structures, charge carriers, secondary metabolism, growth hormones, and signaling, etc. The ROS produced in plant cells under abiotic stress conditions damage biochemical constituents and affect physiological activities in the plants. Plants face abiotic stresses, and micronutrients protect them as being constituents of several enzymes [such as CAT, APX, SOD (Zn-SOD, Zn-Cu SOD, Fe-SOD, Mn-SOD] involved as antioxidants in the defense system. The study concluded that attention to the status of micronutrients in both soil and plants may assist in the management of abiotic stresses to achieve normal growth and yield of plant products.

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Chapter 7

Phosphorus Nutrition: Plant Growth in Response to Deficiency and Excess

Hina Malhotra, Vandana, Sandeep Sharma, and Renu Pandey

Abstract Phosphorus (P) is an essential element determining plants' growth and productivity. Due to soil fixation of P, its availability in soil is rarely sufficient for optimum growth and development of plants. The uptake of P from soil followed by its long-distance transport and compartmentation in plants is outlined in this chapter. In addition, we briefly discuss the importance of P as a structural component of nucleic acids, sugars and lipids. Furthermore, the role of P in plant's developmental processes at both cellular and whole plant level, viz. seed germination, seedling establishment, root, shoot, flower and seed development, photosynthesis, respiration and nitrogen fixation, has been discussed. Under P-deficient condition, plants undergo various morphological, physiological and biochemical adaptations, while P toxicity is rarely reported. We also summarize the antagonistic and synergistic interaction of P with other macro- and micronutrients.

Keywords Abiotic stress · Macronutrients · Nutrient deficiencies · Plant metabolism · Soil fertility

7.1 Introduction

Next to nitrogen (N), phosphorus (P) is a vital nutrient for plant growth and productivity. Its concentration in plants ranges from 0.05% to 0.5% of total plant dry weight. Though concentration of P in soil is 2000-fold higher than the plant, its fixation in the form of aluminium/iron or calcium/magnesium phosphates renders it unavailable for uptake by plants. Hence, plants often face the problem of P deficiency in agricultural fields. Diagnosing its deficiency is a tedious task, since crops generally display no visual symptoms at an early stage. Its deficiency is often confused with N since the veins of young leaves appear red under both deficiencies. However, no general chlorosis is seen in P-deficient plants. P deficiency reduces

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plant growth which is attributed to either decrease in photosynthesis or increase in energy investment. Its limitation negatively impacts crop yield and quality. It has been estimated that P deficiency reduces the crop yields on 30–40% of the world's aerable land. This necessitates the use of a large amount of phosphatic fertilizers to correct its deficiency. The phosphorus use efficiency (PUE) is 15–20% in agricultural fields indicating that most of the soil-applied P remains unavailable to plant and leaches into ground and surface water leading to eutrophication (Correll 1998; Smith 2003).

Phosphorus plays an important role in an array of cellular processes, including maintenance of membrane structures, synthesis of biomolecules and formation of high-energy molecules. It also helps in cell division, enzyme activation/inactivation and carbohydrate metabolism (Razaq et al. 2017). At whole plant level, it stimulates seed germination; development of roots, stalk and stem strength; flower and seed formation; crop yield; and quality. In addition, availability of P increases the N-fixing capacity of leguminous plants. Hence, P is essential at all developmental stages, right from germination till maturity.

Phosphorus is an important constituent of energy-rich compounds, including adenosine triphosphate (ATP), cytidine triphosphate (CTP), guanosine triphosphate (GTP), uridine triphosphate (UTP), phosphoenol pyruvate and other phosphorylated intermediate compounds. Hence, it supplies energy to drive various cellular endergonic processes. Being a constituent of nucleic acids (DNA, RNA), it is essential for reproduction and protein synthesis. In order to maintain its role under inorganic phosphate (Pi-deprived conditions), plants undergo various morphological, physiological and biochemical adaptations. These include alterations in root architecture, formation of cluster roots, shoot development, organic acid exudation and alternative glycolytic and respiratory pathways (Vance et al. 2003). In this chapter, we present an overview of the uptake, translocation and the role played by P in various processes both at cellular and whole plant level.

7.2 Uptake, Long-Distance Transport and Compartmentation of Phosphorus

Uptake is the first step of the pathway involved in the movement of any element from soil to roots and other plant parts. The availability of P in soil solution is largely decided by soil components, including soil pH, texture, concentration of P, metals and anions (Sanyal and De Datta 1991; Hinsinger 2001). The strong interaction of P with soil components favours the flow of P from soil to roots via diffusion, rather than by mass flow. Two pools of P occur in soil, organic (P_{org}) and inorganic (P_i). About 20–80% of the soil P exists in organic form, of which inositol hexaphosphate (phytic acid) is a major component. Rest of the P is present in inorganic form. The activity of soil microbes releases the immobile forms of P to soil solution which is then made available to the plants. Uptake of P is largely favoured between pH 5.0

and 6.0 where it predominates in the monovalent form ($H_2PO_4^-$) (Furihata et al. 1992). Various inorganic forms of P, viz. $H_2PO_4^-$, HPO_4^{2-} and H_3PO_4, occur in soil solution at a concentration of 0.1–10 μM, which is far lower than in plant tissue (5–20 mM) (Hinsinger 2001; Shen et al. 2011). Due to concentration difference between soil and plant, P is actively taken up by transporters present in root plasma membrane against the concentration gradient. Moreover, to increase P uptake, plant roots and microbes excrete various organic acids and extracellular phosphatases, thereby acidifying the rhizosphere and causing easy movement of P inside the root system (Comerford 1998; Hinsinger 2001). After entering the root surface, P follows a symplastic route to reach xylem and then from xylem to aerial parts of the plant. The inter- and intracellular transport of P from xylem to the cytoplasm and further to vacuole is an energy-dependent process (Ullrich and Novacky 1990).

Phosphorus uptake and transport is mediated by the presence of high- and low-affinity transport systems that vary in their Michaelis-Menten constant (K_m) values and operate at low and high P concentrations, respectively (Furihata et al. 1992; Smith et al. 2000; Guo et al. 2002). To prevent membrane hyperpolarization, the transport of P is accompanied by one or two protons or singly (Na^+) or doubly charged cation (Reid et al. 2000; Sakano 1990; Schachtman et al. 1998). Many P transporters have been identified in *Arabidopsis* (PHT1–4), barley (*Hordeum vulgare* PHT1), rice (*Oryza sativa* PHT1) and wheat (*Triticum aestivum* PHT1 and 2) which are involved in the uptake of P from soil and translocation from root to xylem, phloem, leaf, seed, chloroplast, mitochondria and Golgi body (Rausch and Bucher 2002; Miao et al. 2009; Huang et al. 2011; Liu et al. 2013). These are primarily expressed in root and shoot vascular system (Hasan et al. 2016). Many genes, including transcription factors and miRNA, are induced by phosphate starvation (IPS) and aid in the regulation of P homeostasis. These include phosphate responsive (PHO), an E3 ligase (SIZ1), phosphate starvation response (PHR), phosphate transporter traffic facilitator (PHF), WRKY, ZAT6 and miR399 (Miura et al. 2005; Devaiah et al. 2007; Liu et al. 2010a; Bayle et al. 2011; Lin et al. 2014; Wang et al. 2014; Su et al. 2015). However, the transporters involved in recycling of P from older to young leaves are not fully understood. Also, the genetic regulation, temporal dynamics and contribution of these transporters to crop tolerance are poorly known under low P conditions. Hence, further studies are needed to attain the complete understanding of the mechanism underlying P uptake, utilization and transport under P-deficient conditions.

Pi is important in many enzyme-catalysed reactions inside the cell cytoplasm. Hence, maintenance of its concentration in stable form is extremely essential. It constitutes 0.05–0.5% of the plant dry weight, which is far lower than that of N and K (Vance et al. 2003). The Pi pool is determined by various factors, such as pH of cellular compartment and chemical form and functional behaviour of P. For example, in slightly basic cytoplasm, Pi is equally partitioned between $H_2PO_4^-$ and HPO_4^{2-}, while more acidic vacuole and apoplast contain $H_2PO_4^-$ as the dominant form. The chemical form of P, as P-esters or P-lipids, changes with tissue type, age and P availability. The existence of P species also varies with the functional property, viz. metabolic, storage or cycling form. The cellular compartmentation of P has been studied with various radioactive and NMR spectroscopy techniques (Bieleski 1973; Ratcliffe 1994). These studies have confirmed the presence of 1–5% of the total Pi in cytoplasm while vacuole being the major storage site of P.

7.3 Phosphorus Deficiency and Excess

Eroded, weathered and calcium carbonate-rich soils are the common sites of P deficiency. About 80–90% of the soil P is unavailable to the plant due to its fixation as insoluble Ca-P, and hence plant P deficiency is a common problem. Young plants have a higher demand of P in comparison to mature plants which is why the deficiency symptoms are more prominent in the former. Under low P conditions, the plant appears stunted with dark green foliage and reduced leaf surface area. Decreased leaf expansion and hence smaller leaves occur as a result of the reduced cell division and enlargement. The older leaves acquire purplish pigmentation due to more anthocyanins synthesis under limited P conditions. Other symptoms include upward tilting and curling of leaves and brown internal specks in tubers. Plant maturity is also delayed under P limitation; however, these changes vary with the crop species involved (Peaslee 1977). The reduction in shoot growth is comparatively higher than the root growth, hence resulting in a lower shoot-to-root ratio.

Plants respond to P limitation by undergoing various physiological, biochemical and metabolic changes. P-deficient leaves allocate more carbon (C) from shoots to roots, thereby enhancing the overall root growth. Being the primary source of nutrients for plant growth and development, roots respond largely to P availability. To cope up with P limitation, roots induce various chemical and biological changes, which intensify the availability of soil P (Hinsinger 2001). The major ones include alterations in root length, biomass, formation of cluster roots and release of organic substances for more P availability.

Higher concentration of P is often found in the topsoil and it decreases with soil depth. Many studies depicted changes in the root architecture, including morphology, topology and distribution patterns, which helps to facilitate the uptake of P from topsoil (Charlton 1996; Ge et al. 2000; Liao et al. 2001; Lynch and Brown 2001; Williamson et al. 2001). These changes include reduction of primary root length while enhancement of lateral root density, root biomass, root hair density and length, formation of cluster roots, along with greater root penetration capacity (Jungk 2001; Williamson et al. 2001; Péret et al. 2011). These changes are induced by alteration in carbohydrate distribution between roots and shoots as well as by signalling of hormones, sugars and nitric oxide (Nacry et al. 2005; Vance 2010; Wang et al. 2010). In addition to alterations in root architecture, other changes include acidification of rhizosphere, exudation of low molecular weight organic acids, secretion of acid phosphatases and photosynthesis-related enzymes and symbiotic and free-living associations with mycorrhizal fungi and plant growth-promoting bacteria (Neumann and Römheld 2002; Singh and Pandey 2003; Chen et al.

2006; Smith and Read 2008; Zhang et al. 2010; Vengavasi and Pandey 2016b). Exudation of carboxylates (citrate and malate) enhances the mobility of sparingly soluble P by chelation and ligand exchange (Vance et al. 2003; Hinsinger et al. 2005; Wang et al. 2007). The C required for increased organic acid synthesis is provided by both photosynthetic CO_2 fixation as well as by CO_2 fixation in root. Enhanced activities of phosphoenolpyruvate carboxylase (PEPC), malate dehydrogenase (MDH) and citrate synthase (CS) and reduced activities of aconitase (AC) have been reported in various crops (Neumann et al. 1999; Uhde-Stone et al. 2003; Vengavasi et al. 2016). As a result of increased organic acids secretion under P deficiency, root acidification might occur by the release of protons that decreases the rhizospheric pH by 2–3 units (Marschner 1995; Yan et al. 2002; Vengavasi and Pandey 2016a). This increases the availability of sparingly soluble soil P. However, the release of exudates might reduce the efficiency of P mobilization (Shen et al. 2005) which stresses on the need to reconsider such assumptions to systematically understand the interaction of soil P-rhizosphere-carboxylates.

Secretion of phosphatases under P deficiency catalyses the hydrolysis of organic P to increase its mobilization. This is accompanied by an enhanced catalytic activity of plasma membrane H^+ATPase (Yan et al. 2002). Also, their activity is greatly determined by the pH, microorganisms and substrate availability in soil (George et al. 2005). Soil P is successfully mobilized in the presence of phosphate-solubilizing bacteria and fungi which do so by any of the above-mentioned chemical changes (acidification, release of exudates and enzymes) (Jones and Oburger 2011).

Along with increased P mobilization and uptake, plants adapt to P deficiency by conserving internal Pi pools and adopting alternative glycolytic pathways to bypass the requirement of adenylate and Pi-dependent steps. The plant metabolism under P deficiency is switched from primary to secondary. This involves the enhanced synthesis of various secondary metabolites including, flavonoids, indole alkaloids, polyamines, anthocyanins and phenolics. The enzymes, 3-deoxy-D-arabino-heptulosonate-7-phosphate synthase (DAHP), phenylalanine ammonia-lyase, chalcone synthase, chalcone isomerase, 4-coumarate-CoA, cinnamoyl-CoA and cinnamyl alcohol dehydrogenase, are shown to be upregulated under P-deficient conditions. Rather than consuming P_i, secondary metabolism functions in recycling large amounts of P_i from phosphate esters and producing excess of reducing equivalents. Thus, under P deficiency, the acidification of cytosol activates the alternative oxidase (AOX) and secondary metabolite pathway, which together causes the accumulation of reducing equivalents.

To prevent the inhibition of photosynthesis under P deficiency, plants undergo alterations in their thylakoid membrane composition. This reduces the need for membrane-bound Pi, thus making it available for photosynthesis. The phospholipids in the membrane are replaced by sulpholipids by upregulation of sulpholipid-synthesizing enzymes, SQD1 and SQD2 (Nakamura et al. 2009; Nakamura 2013; Lal 2015). This helps to conserve P along with maintaining the membrane integrity.

Phosphorus limitation induces the synthesis of acid phosphatase enzymes (APases) in plants (Duff et al. 1994; Baldwin et al. 2001). Root-exuded APases are implicated in the acquisition of P from soil organic P-esters. In addition to root-exuded APases, intracellular APases function in the remobilization of P from senescent tissue. This is an efficient mechanism to provide additional P for plant growth under low P stress. Root-exuded or extracellular APases appear to be much more stable than intracellular forms (Goldstein et al. 1988; Duff et al. 1989, 1991; Miller et al. 2001). With increased root uptake and translocation of P to shoot, excess P tends to accumulate in the older leaves, thereby causing Pi toxicity (Dong et al. 1998; Aung et al. 2006). Increased concentration of P inside older leaves also leads to more uptake of N which delays the formation of reproductive organs.

7.4 Structural Role of Phosphorus

In the plant tissues, P exists in either of the two forms: free inorganic orthophosphate form (Pi) or as organic phosphate esters. P is compartmentalized within the plant cells depending on its total concentration. The metabolically active Pi form is located in the cytoplasm, while excess of P is stored in the vacuole from where it is supplied to cytoplasm on cellular demand. Hence, the vacuole has a buffering function and fulfils the P demand of the cytoplasm under P deprivation. The esterified P exists in various forms, nucleic acids, phospholipids, phosphorylated metabolites and proteins. For most of the crops, the optimum P concentration is <4 mg g^{-1} DW. Of all the pools of P, RNA forms the largest, followed by lipids, esters, DNA and metabolically active Pi.

7.4.1 Nucleic Acids: Genetic Transfer

Phosphorus is a vital component of nucleic acids (DNA and RNA) that carry the genetic information from one generation to the next. They form the largest pool of total organic P in a plant and ranges from 0.3 to 2.0 mg P g^{-1} DW in various crops. Of the nucleic acid pool, 85% is contributed by RNA (majorly rRNA) and the rest by DNA. There are evidences of increased RNA concentration and hence protein synthesis with the increased supply of P to the plant (Elser et al. 2010; Suzuki et al. 2010).

7.4.2 Sugar Phosphates

Sugar phosphates are the Pi esters formed by the phosphorylation of monosaccharide sugars after their reaction with ATP. These phosphorylated compounds are the prime intermediates of photosynthesis and in the synthesis and breakdown of starch. These compounds include phytic acid, glucose-6-phosphate and dihydroxyacetone phosphate. In addition, they are important constituents of glycolysis and respiratory reactions.

7.4.3 *Phospholipids: Membrane Component*

Phospholipids are an essential component of cell membranes. These consist of lipophilic and hydrophilic regions. The electric charge of the hydrophilic region helps to make interactions between membrane and the charged ions. In P-deficient cells, phospholipids are often replaced by sulpholipids and/or galactolipids (Gaude et al. 2008; Byrne et al. 2011). This replacement has no major effect on proton permeability but might increase the leakage of electrolytes responsible for chilling tolerance.

7.5 Growth and Developmental Role of Phosphorus

7.5.1 *Seed Germination*

Seed P content is an important factor for seed germination and improved seedling vigour. Seed P is the only P available to plants at the time of germination and helps in supporting the early seedling growth. Although this P pool is of minor importance for mature plant, it has a prime role for the nutrition and faster establishment of young seedlings. After seed germination, plant requirement of P is met from growing media through roots. Zhu and Smith (2001) found increased soil P uptake by high P wheat seeds as compared to low P seeds. This was mainly due to the better development of root system in seeds of high P reserves (Zhu and Smith 2001). During early days of seedling development, seed phytate P is hydrolysed, and non-phytate P is then remobilized to support the growth of maize seedling (Nadeem et al. 2011, 2012). However, in some reports, lower seed P concentration showed no variation in seedling vigour, plant biomass and yield when compared to high seed P plants, though some genotypes were found to be sensitive (Rose et al. 2012; Pariasca-Tanaka et al. 2015). This implies that an optimum seed P concentration is sufficient for seed germination, and hence, higher P concentration in seeds might be of no use.

7.5.2 *Increasing Root and Shoot Strength*

Phosphorus is an important element affecting the growth of plants right from the cellular to whole plant level. These growth parameters include plant height, leaf area, leaf number and shoot dry biomass. It plays an important role in cell division and cell enlargement (Assuero et al. 2004). For timely appearance and development of tillers in crop plants, P is essential (Rodriguez et al. 1998). The P-deprived leaf cells are found to be smaller than P-sufficed cells. Limited cell divisions and enlargement results in overall reduction in the shoot biomass. However, the reduction in leaf expansion is not accompanied by a reduction in leaf dry weight. The leaf dry weight is found to be higher due to the increased starch or celluloses and hemicelluloses. In general, the plant growth parameters are found to be more sensitive to P availability than the photosynthesis (Halsted and Lynch 1996). This is due to the reduced demand of assimilates by sink. The transport of assimilates from leaves to roots and stems increases, while their utilization is decreased. This shows that C utilization rather than C availability is the prime reason of reduced photosynthesis. Also, no correlation has been reported between leaf photosynthetic rate and growth response under Pi-limiting conditions. Increase in root biomass is considered as an important adaptive strategy by plants under P-deficient conditions with an aim to explore for more P. But it is evident only at the beginning of P-limited environment. Under long-term Pi-deficient conditions, the relative growth rate decreases as a result of reduced ATP concentration in roots (Gniazdowska et al. 1998). However, genotypes with greater PUE tend to have higher root biomass and lower rates of respiration than genotypes with lower PUE under P deprivation. This is suggested as a way to maintain greater root biomass without any increase in overall root C costs.

7.5.3 Flower and Seed Formation

Phosphorus plays an essential role in improving the reproductive growth of plants, including flower and seed formation. P contributes to the production of anthocyanins in flower stalks, which was found to decrease under P-deficient conditions. This was attributed to decreased activities of phenylalanine ammonia-lyase (PAL) and chalcone isomerase (CHI) (Chen et al. 2013). Large quantities of P are found in seeds and fruit where it is believed to be essential for seed formation and development. In cereal crops such as rice and wheat, majority of P taken up by plants is stored in seeds. Thus, an inadequate supply of P can reduce seed size, seed number and viability. Optimum P concentration in soil increases the seed number, seed dry matter, seed yield and harvest index. Coating of seeds with 7 g per kg of monosodium phosphate enhanced the growth and yield of soybean plants (Soares et al. 2016). Also, Ma et al. (2002) compared the response of white lupin (*Lupinus albus*) to various P concentrations in soil. They found that low soil P (5, 10 or 15 mg per kg) had a negative impact on flowering time and flower number but no differences were recorded with P supply higher than 20 mg per kg. Higher P concentration (25–40 mg kg^{-1}) succeeded in increasing the number of pods and hence yield in soybean (Ma et al. 2002). P is a component of phytin, a major storage form of P in seeds. Various crops differ in their concentration of phytate in seed. About 75% of the total P in rice, wheat and maize is stored as phytin or closely related compounds, while inorganic phosphate and cellular-P range from 4–9% to 15–25%, respectively (White and Veneklaas 2012).

7.6 Energy Transfer Reactions by Phosphorus

7.6.1 Energy-Rich Phosphates

Phosphorus is a vital component of high-energy bonds, including phosphoanhydride, acyl phosphate and enol phosphate and plays an important role in cellular metabolism. These high-energy phosphate-containing compounds transfer the energy to acceptor molecules, thereby serving as sources of crucial cellular processes. It plays an important role in photosynthesis right from the seedling growth till grain formation and maturity.

Phosphoanhydride bond is the bond between two phosphoric acid molecules. ATP, energy currency of cell, contains three phosphoryl groups ($-PO_3^{2-}$) which are linked by two high-energy phosphoanhydride bonds and one phosphoester bond (Fig. 7.1). The hydrolysis of ATP releases a large amount of free energy which is utilized in various cellular processes of the organisms. The hydrolysis of γ, β and α-phosphate releases an energy of 34.0, 27.2 and 13.8 kJmol^{-1}, respectively. ATP is utilized in many cellular processes, including synthesis of macromolecules, membrane phospholipids and nutrient transport against a concentration gradient. Other similar phosphoanhydride bonds are present in di- and triphosphate-containing molecules in guanine, cytosine, uracil and thymine nucleosides. GTP and UTP are important electron donors in gluconeogenesis and saccharide metabolism, respectively.

The bond formed between phosphate and hydroxyl group attached to double-bonded C is the enol phosphate bond. During glycolysis, phosphoenol phosphate is formed from 2-phosphoglycerate. It is the highest energy liberating bond, releasing energy equivalent to 61 kJ mol^{-1}. The reaction of phosphate with carboxylic acid forms the acyl phosphate bond, liberating an energy of 49 kJ mol^{-1} on hydrolysis. A glycolysis intermediate, 1,3-bisphosphoglycerate, is an example of acyl phosphate bond which transfers its phosphate group to ADP to form ATP and 3-phosphoglycerate.

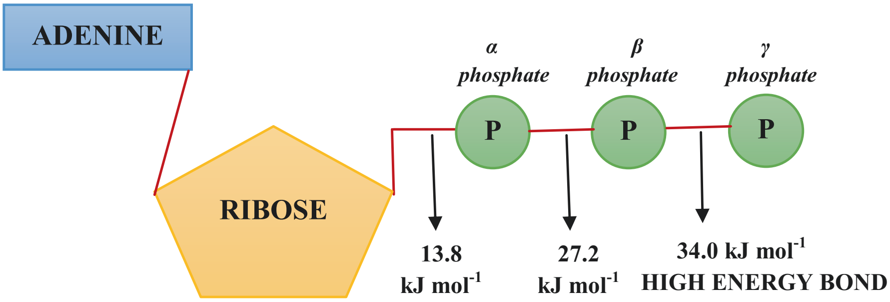

Fig. 7.1 Structure of adenosine triphosphate

7.6.2 Nutrient Transport

Nutrient transport through membranes of root, leaf and other plant organs is an energy-dependent process which is carried out by adenosine triphosphate (ATP) or other high-energy phosphorylated compounds. This is due to the impermeable nature of the plasma membrane acting as a protective layer for cells. Hence, the transport of nutrients acts against a concentration gradient through specific transport proteins spanning the plasma membrane. Once inside the cell, nutrient easily moves to another cell via symplastic or apoplastic pathway. Symplastic to apoplastic movement for long-distance transport of nutrients occurs through epidermal and endodermal cells, respectively. H^+-ATPase is a major plasma membrane-bound proton pump in plants that imports nutrient into the cell along with the export of H^+ by utilizing a three-phosphate-containing molecule, ATP (Sondergaard et al. 2004).

The first transport barrier for any nutrient is the root. Plant roots contain specialized thin protrusions, called root hairs, which increase surface area for the uptake of nutrients. After entering into the root symplast, nutrients are then transported to xylem and phloem to ultimately reach leaves, fruits and seeds. High amounts of plasma membrane H^+-ATPase are detected in the epidermal and endodermal root cells, xylem and phloem cells to facilitate the transport of nutrients by utilizing ATP and exporting H^+ (Parets-Soler et al. 1990; Jahn et al. 1998; Zhang et al. 2004).

7.7 Physiological Role of Phosphorus

7.7.1 Photosynthesis and Carbon Utilization

The photosynthetic process relies highly on the availability of P. The primary substrates for photosynthesis include Pi, CO_2 and H_2O that utilizes light energy in the presence of chlorophyll forming sugars and ATP. This ATP serves as a driving force to carry out various metabolic reactions within the plant and sugars help in the generation of other structural and storage components.

During photosynthesis, the initial step is photophosphorylation through which Pi combines with ADP forming ATP, along with the discharge of a proton gradient through an ATPase into the chloroplast stroma. The atmospheric CO_2 is fixed in the chloroplast via photosynthetic carbon reduction (PCR) cycle, consuming ATP. For every three molecules of CO_2, nine Pi are consumed forming three molecules of O_2. Out of these nine Pi, eight are released into the chloroplast via PCR cycle, while one is exported from chloroplast to the cytosol in the form of triose phosphate (triose-P) where it is converted into sucrose, releasing and recycling P_i. This P is now available to move back into the chloroplast to further form triose-P in chloroplast.

In chloroplast, the inner envelope is impermeable to hydrophilic solutes including Pi and other phosphorylated compounds. Hence, the counter-exchange of various metabolites such as triose-P, 3-phosphoglyceric acid (3-PGA) and Pi across the envelope is carried out via Pi translocators (Heber and Heldt 1981; Flugge and Heldt 1984). Through these Pi translocators, the photosynthetically fixed C is transported from chloroplast to cytosol in the form of triose-P and in exchange of Pi. Pi released in the cytosol during sucrose synthesis is shuttled back into the chloroplast via Pi translocator for the synthesis of ATP. External P levels regulate photosynthesis by altering the function of the Pi translocator. Low P levels in cytosol reduce the flow of triose-P into the chloroplast, thereby decreasing the Pi release from sucrose synthesis in chloroplast and reducing ATP production required for PCR cycle. Also, Pi translocator participates in the transport of ATP and NADPH produced during photosynthesis to the extra-chloroplastic compartments.

Changes in Pi availability in cytoplasm alters the activation of enzyme (RuBisCO, sedoheptulose-1,7-bisphosphatase and fructose-1,6-bisphosphatase) and amounts of intermediates of the PCR cycle. The concentration of phosphorylated metabolites, including RuBP, PGA, triose-P, FBP, F6P, G6P, adenylates, nicotinamide, nucleotides and Pi, is reduced under P deficiency. This happens due to the decreased C supply as most of the C is diverted for starch production. However, the cytosolic concentration of P remains stable due to the availability of P in vacuole, and hence the vacuolar pool is found to lower under P-deficient conditions. The requirement of Pi for activation of RuBisCO has been shown by many authors (Heldt et al. 1978; Bhagwat 1981). Sufficient concentrations of Pi in chloroplast inhibit the activities of enzymes fructose-1,6-bisphophatase, sedoheptulose-1,7-bisphosphatase and ribulose-5-phosphate kinase. Under low cytoplasmic P concentration, photosynthesis is inhibited due to end product inhibition. The total organic and inorganic Pi concentration remains constant inside the chloroplast. Hence, low Pi concentration corresponds to high triose-P that limits photosynthesis. These together inactivate RuBisCO due to the build-up of various metabolites such as ribulose-5-P and PGA. Also, low Pi concentration limits photosynthesis by decreasing the ATP/ADP ratio by reducing photophosphorylation that further limits the rate of C fixation in PCR cycle. It has been observed that Pi deficiency leads to a decrease in Pi concentration in stroma which limits photophosphorylation, thereby inhibiting the photosynthesis (Robinson and Giersch 1987).

Phosphorus is essential in maintaining the photosynthetic machinery that includes PSI, PSII, LHCP, cyt-f, cyt-b and antenna mobility (Rychter and Rao 2005). As mentioned above, P is an important constituent of the thylakoid membrane. Phosphorylation of apoproteins of antenna in thylakoid membrane is an important step in photosynthesis. Under P deficiency, the antenna becomes dephosphorylated due to activation of a phosphatase and a large proton gradient, thereby reducing the mobility of antenna (Horton 1989). The long-term deficiency of P causes the photoinhibition of PSII. The rate of electron transport increases across PSII under P-deficient conditions, and the unused electrons are diverted to photorespiration, thereby reducing CO_2 fixation. The increase in photorespiration plays an important role in increasing the availability of Pi for photosynthesis.

Pi plays an important role in starch biosynthesis inside the chloroplasts. The level of Pi controls the distribution of newly fixed C between starch synthesis in chloroplasts and sucrose synthesis in cytoplasm. Limited Pi supply in chloroplasts shifts the flow of C towards starch. This is achieved through the stimulation of key enzyme in starch biosynthesis, ADP-glucose pyrophosphorylase under low Pi and high triose-P levels (Nielsen et al. 1998). Likewise, increased Pi concentration in stroma induces the breakdown of starch. Starch degrades to form glucose-1-phosphate which is further converted to triose-P or PGA through oxidative pentose phosphate pathway or phosphofructokinase, respectively. This has been confirmed by various kinetic studies (Pettersson and Ryde-Pettersson 1989; Preiss 1994).

The biosynthesis of sucrose is a Pi-regenerating step, which occurs in cytoplasm from triose-P that is exported from the chloroplast. The cytosolic triose-P is first converted to hexose-P and then to sucrose. FBPase, sucrose-phosphate synthase (SPS) and UDP-glucose pyrophosphorylase are the key enzymes regulating sucrose biosynthesis in cytoplasm (Huber and Huber 1992, 1996; Stitt et al. 1983). Pi is a negative regulator of these enzymes but a positive regulator of fructose-6-phosphate-2-kinase. Four molecules of triose-P are needed to form one molecule of sucrose, and four Pi are liberated in this process. The release of Pi in this process maintains the import of triose-P in cytoplasm through Pi translocator via the counter exchange of Pi. Under conditions of low sucrose synthesis, triose-P remains in the chloroplast to support starch synthesis. Low sink strength lowers sucrose synthesis and hence increases the accumulation of triose-P in chloroplast to synthesize starch, thereby restricting photosynthesis. For each molecule of sucrose formed, four Pi molecules move into the chloroplast. Defective sucrose synthesizing machinery will lead to decreased formation and hence transport of triose-P from chloroplast. The accumulated photosynthates in chloroplast induce the conversion of fructose-6-P (in PCR cycle) to starch. Hence, Pi levels regulate the distribution of C between starch and sucrose synthesis. Also, it regulates the partitioning of photosynthates between various plant tissues. Under P deficiency, the low sink demand limits the photosynthesis. Pi is released from sucrose synthesis with the help of phosphatase that makes Pi available for entry into the chloroplast to form triose-P, and little or none will be available for storage as starch. During low sink demand, excess triose-P is stored as starch, thus reducing the rate of photosynthesis.

Phosphorus plays a vital role in the respiratory processes of the plant. Under P-deficient conditions, roots tend to respire via an alternative non-phosphorylating pathway. This cyanide-resistant respiratory pathway results in reduced production of ATP and ADP which affects the energy-dependent processes of the plant (Rychter and Mikulska 1990; Rychter et al. 1992). This is achieved by skipping ATP-dependent steps in glycolysis and activating PPi-dependent phosphofructokinase, non-phosphorylating NADP-dependent glyceraldehyde-3-P dehydrogenase, PEPC, NAD malic enzyme and MDH. This successfully bypasses the requirement of enzymes, viz. ATP-dependent phosphofructokinase (PFK), Pi-dependent NAD-dependent glyceraldehyde-3-P dehydrogenase, phosphoglycerate kinase and pyruvate kinase, to conserve ATP pools. The resulting increase in ATP/ADP ratio limits mitochondrial respiration under P limitation. Owing to this, alternative non-phosphorylative respiratory pathways become active that includes rotenone-insensitive

NADH dehydrogenase and cyanide-resistant alternative oxidase (AOX). This leads to an increase in the ratio of NADH/NAD. The levels of respiratory intermediates, viz. hexose phosphates and 3-phosphoglyceric acid (PGA), reduce during P deficiency. The activities of several glycolytic enzymes PFK, NAD-G3P-DH, 3-PGA kinase and PK depend on the concentration of adenylate and Pi. The activities of PFP and non-phosphorylating NAD-G3P-DH, PEP carboxylase and PEP phosphatase have been found to increase under P-deprived conditions.

7.7.2 Nitrogen Fixation

Legumes are a vital source of protein in human diet. They also play an essential role in maintaining soil fertility. The fundamental phenomenon which makes legumes important is their ability to carry out "atmospheric nitrogen fixation". The conversion of non-useable form of nitrogen (N_2) to useable form (NH_3) is done by *Rhizobium* bacteria, which resides in the root nodules of leguminous plants. These bacteria need energy to grow and perform their basic functions. The energy is supplied in the form of P rich molecule, ATP. This energy-rich molecule gets converted into ADP with simultaneous release of inorganic phosphate providing the energy. At least 16 molecules of ATP are hydrolysed for each molecule of N_2 reduced.

$$N_2 + 8e^- + 8H^+ + 16\,ATP + 16\,H_2O \leftrightarrow 2NH_3 + H_2 + 16\,ADP + Pi$$

In addition to acting as a source of energy, P helps in increasing the density of rhizobial bacteria in soil. For root nodule formation, root hairs must get infected by these bacteria. The site where these bacteria infect root hair becomes the site of nitrogen fixation. As discussed above, P is one of the essential nutrients for root growth promotion. P deficiency not only affects plant growth but also highly impacts the rate of nitrogen fixation by causing a reduction of root nodules (Bonetti et al. 1984). In pea plants, it has been observed that an increase in P supply increases the biomass of root nodules (Jakobsen 1985).

7.8 Crosstalk of Phosphorus with Other Nutrients

The presence of P affects the availability of one or more of other nutrients in soil. Interaction of P with both macro- and micronutrients is well studied, and it can be either synergistic or antagonistic. Soil analysis before sowing helps in the detection of limiting factors in soil, and giving optimum P levels in early stage can help in enhanced availability of other nutrients, thereby increasing crop yield.

7.8.1 Macronutrients

Nitrogen (N) plays a vital role in plant metabolism and growth. The interaction between P and N has been found to be synergistic. The ammonical-N fertilizer increases the P availability to plant. P is one of the essential nutrients that help in nitrogen fixation, along with efficient use of N by plants. The combined application of N and P increased the sorghum yield to 93 bu/ac, while N alone resulted in a yield of 71 bu/ac (71 bushel/acre = 71 × 67.25 = 4774.75 Kg/ha) (Schlegel and Bond 2017).

Phosphorus and K are required for proper growth of plant under control and stressed conditions. For better corn yield, presence of both P and K is found to be must. They together enhanced the grain yield by 64 bu/ac as compared to 38–41 bu/ac when each was applied alone (Usherwood and Segars 2001). Proper ratio of both P and K is essential for obtaining high yield in corn.

An antagonistic interaction exits between sulphur (S) and P in moong seeds. It has been shown that combined application of S and P decreased the grain yield and quality. In a greenhouse experiment, application of 40 ppm S depressed the P content of vegetative portion by 18% and grains of moong by 12% (Aulakh and Pasricha 1977). Magnesium (Mg) helps in root formation, chlorophyll and photosynthesis. One of the most important functions regulated by Mg is activation of kinase enzyme and transfer of phosphate group.

7.8.2 Micronutrients

The interaction of P with micronutrients has been reported in a wide variety of crops. Due to better understanding of functions of micronutrients in crop plants, significance of micronutrients in crop production has increased. One of the main reasons for this is the availability of better analytical techniques. Micronutrients play an important role in uptake and utilization of essential plant nutrients.

The interaction between P and boron (B) has been found to be synergistic in maize grown in refined sand (Chatterjee et al. 1990). In lettuce plants, increase in 1000 seed weight (from 2.06 to 3.01 g) was observed due to interaction between B and P (Chowdhury et al. 2015). On the other hand, when different levels of copper (Cu) were sprayed on leaves, a positive interaction was found between P and Cu in lettuce (De Iorio et al. 1996). Iron (Fe) is found in abundance in the earth's crust, but still it is often a limiting resource for growth. This is mainly due to its low availability. Fe deficiency can be diagnosed as interveinal chlorotic symptoms in young leaves. Fe and P show antagonistic interaction in plant nutrition. It has been noticed that P also affects the genes responsible for iron regulation (Zheng et al. 2009). Optimal levels of molybdenum (Mo) improve utilization as well as increase P uptake. In *Brassica napus* positive interaction between Mo and P has been detected. It has been found that both Mo and P promote plant growth when applied together. This is because Mo and P have beneficial effects on each other's' absorption and translocation (Liu et al. 2010b). P and zinc (Zn) show antagonistic interactions in soil or inside the plant. In corn seedlings grown in sandy soil, absence of a significant Zn-P interaction has been seen, but high P supply reduces Zn shoot content (Drissi et al. 2015). At gene level, high levels of P downregulates high-affinity Zn transporter, thus adversely affecting Zn mobilization within the oat seedlings (Huang et al. 2000).

7.9 Conclusions

Yield losses due to global climatic change and mineral nutrient deficiency are the major concerns for researchers worldwide. The role of P in essential metabolic processes including growth, photosynthesis, respiration and nitrogen fixation has been well documented in various studies. Limited availability of P in soil reduces the uptake by plant and causes plant P deficiency, thus affecting its overall growth and development. To tackle P deficiency, plants have developed numerous morphological, anatomical, physiological and metabolic processes. However, to develop plants with better adaptability to P stress and enhanced P use efficiency, collaborations between physiologists, geneticists and breeders are urgently required. Future research trials should focus on improving the understanding of P uptake, utilization and transport mechanisms under low P environment. Further, extensive research is required in field of root biology, along with identifying and enhancing gene expression for improved P acquisition and use efficiencies.

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Chapter 8
Role of Potassium in Governing Photosynthetic Processes and Plant Yield

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Abstract The potassium (K) role is very important for plants; indeed it is an essential macronutrient and has a several metabolic functions, and one of them is implicant on photosynthesis process, growth, and development and stress resistance under K deficiency. Although the K requirement changes during phenological plant stages and due to environmental factors, we, in an undifferentiated way, have put the focus specifically on the role of potassium in the Hill reaction and Calvin and Benson cycle of the photosynthesis. In the Hill reaction, the main role is associated with generation of NADPH and ATP, together with ionic equilibria, electron transport, and proton-motive force. In the Calvin and Benson cycle, the main role is

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associated with CO_2 fixation and sugar production and transport and hence with partitioning of photoassimilates. Special attention, we have put in the regulation of photoassimilates and its distribution as future directions, because under K deficiency, the biosynthesis of sugar, transport, and distribution in the plant are limited. More studies at the molecular level are required to elucidate mechanisms and regulatory point that underlie of the complex network of biochemical relationships.

Keywords Hill reaction · Calvin and Benson cycle · Photoassimilate distribution

8.1 Potassium Requirements in Plants

Potassium is involved in numerous metabolic and biochemical processes in plant cells (Rengel and Damon 2008; White 2013) including regulatory and transport mechanisms (Adams and Shin 2014). To describe some nutritional characteristic of this element, we considered two contrasting plant species: *Triticum aestivum* L. (monocotyledonous) and *Solanum tuberosum* L. (dicotyledonous). Depending on the spatial and temporal variability, crop species, and fertilizer input (Zörb et al. 2014), tissue K concentration ranges from 8 to 43 g kg^{-1} dry matter (DM), but most common values in the literature are 25–35 g kg^{-1} (Chuan et al. 2013a, b). For many crops, the critical deficiency range is 5–20 g K kg^{-1} (Leigh and Jones 1984; Askegaard et al. 2004; Öborn et al. 2005). The K requirement increases in the reproductive stages (Oosterhuis et al. 2014).

*8.1.1 Wheat (*Triticum aestivum *L.)*

Scanlan et al. (2015a) indicate that uptake of K depends on a dynamic interaction among K availability, soil properties, environmental conditions, and agronomic management. In several wheat organs, but not in mature grains, the K concentration is relatively easy to increase. Wheat is considered a species with a low internal requirement of K, about 29–39 g kg^{-1} for maximum yield (El-Dessougi et al. 2011); in contrast, mature grains contain about 3 g K kg^{-1} DM under a wide range of K supply (Zörb et al. 2014) and over a long term (Merbach et al. 2000; Zörb et al. 2014). Potassium tends to accumulate post anthesis; nevertheless, tissue K concentration decreases during grain development, being the lowest at maturity (El-Dessougi et al. 2011; Zhan et al. 2016).

White (2013) distinguished between uptake efficiency (root capacity to acquire K from soil) and utilization efficiency of K (using an amount of K taken up to produce yield), both influencing K use efficiency when applied to soil as fertilizer. The efficiency of converting K fertilizer into the useful agricultural output, or partial fertilizer productivity (amount of economic product produced per unit of K fertilizer applied), is variable (Naklang et al. 2006). The K fertilization efficiency depends on several factors, including the depth of fertilization (Scanlan et al. 2015b). Studies in China reported values of 23–113 kg grain of wheat per kg of K taken up, representing almost a fivefold variation (Chuan et al. 2013b). Another parameter to consider is the yield per unit of K fertilizer applied (e.g., 5.4 kg grain per kg of K fertilizer applied, Chuan et al. 2013a). Model simulations reported by Chuan et al. (2013b) for wheat in North Central China, under a wide range of rainfall (100–1750 mm) and temperature (−20 to 33 °C) conditions, predicted that 1000 kg of grain requires about 19 kg of K, achieving about 70% of potential wheat yield. In this case, the efficiency is around 53 kg grain per kg of K. According to El-Dessougi et al. (2002), the wheat K efficiency could be attributed to a larger root system and a higher utilization efficiency or lower internal K requirement. Moreover, Rengel and Damon (2008) pointed out that a phenotype may be K-efficient for uptake and utilization based on exudation of organic compounds, large surface area of contact between root and soil, effective translocation of K to maintain adequate cytosolic K^+ concentration, and increase capacity to replace K^+ by Na^+.

*8.1.2 Potato (*Solanum tuberosum *L.)*

In contrast to *T. aestivum*, *S. tuberosum* is a species requiring high K levels for growth and development, which is characteristic of tuber plants, due to the low efficiency of nutrient uptake, because of a relatively shallow root system (Kang et al. 2014; Tein et al. 2014; Zörb et al. 2014). Indeed, the K requirement is greater than that of N and P (Panagiotopoulos 1995; Westermann 2005). The efficiency of agronomic fertilization was about 25 kg DM tubers per kg K in different soil types and management systems, with about a quarter of the yield explained by exchangeable K (Li et al. 2015). Potato may extract 68–184 kg K ha^{-1}, with the highest values under irrigation (Li et al. 2015).

The K application to *S. tuberosum* influences quality characteristics of potatoes, especially potatoes destined for industrial processing (Gerendás et al. 2007; Zörb et al. 2014). An inverse relationship between sugar and K concentration in tubers is important for industrial processing and human nutrition (Westermann et al. 1994). It is interesting to note that K concentration is higher in the peel than in tuber pulp. Adequate K concentration is around 4 g K kg^{-1} tuber DM (Subramanian et al. 2011).

8.2 Potassium and Its Role in Stress Resistance

Potassium is associated with plant adaptation to biotic and abiotic factors. In this chapter, we discuss drought, salinity, and cold (frost). The action of K in resistance to stresses may be both direct and indirect and is dose-dependent (Dordas 2008; Anschütz et al. 2014; Benito et al. 2014; Zörb et al. 2014). The direct responses relate to processes such as photosynthesis and are addressed in the subsequent sections. The indirect responses are related to secondary metabolism activation, including some characteristic metabolites such as oxylipins and glucosinolates detected in *Arabidopsis thaliana* (Troufflard et al. 2010). In the same species, Armengaud et al. (2009) proposed that the first indicator of K deficiency is a direct inhibition of pyruvate kinase activity.

8.2.1 Potassium Effects Under Drought Stress

The primary drought effect is a hyperosmotic stress, whereas the secondary effects include oxidative stress, damage to cellular components, and metabolic dysfunction (Zhu 2016). Evidence that supply of mineral nutrients may alleviate drought stress exists, particularly in sugarcane (*Saccharurn* sp.), where tolerance was related to high concentrations of K and N in leaves and stems (Silva et al. 2017). Cakmak and Engels (1999) indicated that an internal K requirement increases under drought stress because of the high importance of K in photosynthesis, CO_2 fixation, protection of chloroplasts from photooxidative damage, and osmoregulation. Hence, foliar K fertilization can contribute to relieving drought stress in *Triticum aestivum* and *Gossypium hirsutum* (Cakmak 1997; Raza et al. 2014; Saleem et al. 2016). Under drought, plants must reduce their osmotic potential, e.g., by (a) increasing concentration of solutes such as sugars, alcohols, or amino acids or (b) increasing the internal K concentration (if sufficient K is available) as a low-cost alternative to increasing organic solute concentration, emphasizing the importance of K under drought stress (Mengel and Arneke 1982; Hu and Schmidhalter 2005; Chen et al. 2005; White 2013).

8.2.2 Potassium Effects Under Salinity Stress

Salinity is an important constraint for many crops, causing a hyperosmotic and ion toxicity; the secondary effects of salinity include oxidative stress, damage to cellular components, and metabolic dysfunction (Zhu 2016). Understanding the mechanisms that underlie salinity resistance is crucial for development and application of relevant agronomic practices. In *Oryza sativa* salinity caused a photosynthetic rate decrease and reduction in electron transport rate, CO_2 concentration in the chloroplasts, and osmotic leaf potential (Wang et al. 2017).

Potassium deficiency may be one of the consequences of salt stress, exacerbating salt-dependent ROS generation. Hence, an application of K under salt stress might contribute to alleviation, mainly due the reduction in ROS generation and inactivation of superoxide radicals by enhancing the NADPH oxidase activity. This NADPH oxidation may be up to eightfold higher under low K compared with control (Cakmak 2005). Potassium supplementation under salinity stress improved N uptake and assimilation and decreased Na accumulation (decreased K/Na ratio), resulting in a yield increase (Abass and Agarwal 2017). Jha and Subramanian (2016) proposed using bacteria with the ability to solubilize K from insoluble K-bearing rocks to promote plant growth under 2.3–3.5 dS m^{-1} salinity and low availability of P and K. Under these conditions, K supplementation decreased oxidative stress caused by salinity, triggering the enzymatic and nonenzymatic antioxidant systems. A decrease in lipid peroxidation increased the stability of cell membranes, thus enhancing cell performance under stress (Jha and Subramanian 2016). Salinity tolerance in halophytes can be increased by retention of K in the leaf mesophyll cells (Percey et al. 2016). The study in halophytes like a model has been used more frequently, because these species (e.g., *Thellungiella halophile*) do not have multiple tolerance mechanisms like a transgenic species used as a model (Zhu 2001). At the molecular level, the halophyte species group (e.g., *Thellungiella salsuginea*) is different from other species group (e.g., *Arabidopsis thaliana*) by the number of gene copy and appears to be that its strength transcription expression or its stability is related to its differential tolerance. The above has been observed on *SOS1* gene that is considered important in salt tolerance by salt extrusion and internal plant distribution (Shi et al. 2003; Dassanayake et al. 2011).

8.2.3 Potassium Effects Under Cold and Frost Stress

Cold and frost cause inhibition of metabolic and biochemical plant processes, generating osmotic and oxidative stress. These direct and indirect effects influence plant yield (Wang et al. 2013), damaging photosynthetic structures and processes and reducing the effectiveness of antioxidant enzymes (Mittler 2002; Xiong et al. 2002; Suzuki and Mittler 2006). In K-deficient plants, chilling is associated with inhibition of water uptake and freezing-induced cellular dehydration (Zhu 2001). In species with low tolerance to cold and frost, K fertilization contributes to frost tolerance, as shown by lowered electrolyte leakage from young and old leaves (Gómez-Ruiz et al. 2016). The main effect of K in plants under cold and frost stress is a decrease in ROS generation and an increase in expression of the genes associated with biosynthesis of secondary metabolites involved in cold and frost tolerance (Kant and Kafkafi 2002; Cakmak 2005; Devi et al. 2012).

8.3 Role of Potassium in Photosynthesis

8.3.1 The Function of Potassium in Photosynthesis

After N, K is the most abundant element in the photosynthetic tissues (Sardans and Peñuelas 2015). Potassium is relevant to photosynthetic processes because of its impact on chlorophyll fluorescence, RuBisCO activity, and net fixation of CO_2 (Oosterhuis et al. 2013). Potassium is involved in the structural and physiological aspects of the photosynthetic process in *Eucalyptus grandis* (Battie-Laclau et al. 2014). However, in general, the underlying mechanisms behind K effects in photosynthesis are poorly understood; nevertheless, it has been observed that K is related to stomatal aperture, intercellular air spaces, leaf thickness, parenchyma thickness, and specific leaf area, all directly related to the photosynthesis process (Battie-Laclau et al. 2014).

A decrease in K concentration in *Vicia faba* L (from 50 to 20 mM) was associated with a 20% decrease in maximum photochemical efficiency (Fv/Fm). This parameter was also reduced with increased efflux of K^+ from the mesophyll cells of *Spinacia oleracea* L. and *Vicia faba* L (Demmig and Gimmler 1983; Percey et al. 2014). It should be borne in mind that Kranz anatomy and metabolic mechanisms that work as CO_2 concentrators allow a better productivity of C4 than C3 plants. In the last group the CO^2 levels are especially relevant, because produce an immediate export and carbon partitioning differentiated in species like *Panicum* and *Flaveria* (Leonardos and Grodzinski 2000). Sun et al. (2014) in comparative studies of *Zea mays* and *Miscanthus* x *giganteus* pointed out the differences between species in the capacity to coordinate the activities of the C3 and C4 cycles in response to light quality, but it is poorly understood how increased productivity of C4 is affected by nutrients, including K.

8.3.2 Photosynthetic Performance Under Potassium Deficiency

Potassium is an element whose deficiency results in suboptimal functioning of the photosynthetic apparatus (Hart 1970). Potassium deficiency can affect the photosynthetic process in *Glycine max* in dependence on CO_2 concentration (Singh and Reddy 2017). Nevertheless, K deficiency may not always limit photosynthetic rate. At a low K sink demand, Pan et al. (2017) observed in *Brassica napus* L. that the photosynthetic rate did not decrease consistently, where sink strength may be involved in signaling. The same authors observed a negative relationship between photosynthesis and carbohydrate concentration in the low K treatment but not in the optimal K treatment. In this sense, Singh and Reddy (2017) pointed out that K deficiency limited *Glycine max* growth more than the photosynthetic processes. Similar results were observed by Li et al. (2013), where a 25% reduction in the N/K input to strawberry (*Fragaria* × *ananassa* Duch.) was associated with higher leaf intercellular CO_2 concentration than in control. Hence, under K deficiency, the causes of a decrease in the photosynthetic rate may be due to (1) a decrease in mesophyll conductance caused by anatomical alterations in leaves resulting in a decrease in chloroplast surface area per unit of leaf area (Battie-Laclau et al. 2014; Lu et al. 2016), (2) decreased stomatal conductance, and (3) decreased chlorophyll concentration (Weng et al. 2007; Martineau et al. 2017).

The photosynthetic rate is primarily limited by stomatal limitations (conductance) and secondarily by biochemical processes in *Gossypium hirsutum* L. under severe K deficiency (Oosterhuis et al. 2013). Conversely, Jin et al. (2011) pointed

Table 8.1 Effects of K deficiency on photosynthetic processes

Photosynthetic process	Effect	References
	Thermal dissipation increased	Spencer and Possingham (1960) and Weng et al. (2007)
	Electron transfer decreased	
	Photochemical quenching reduced	
	Diminished counterion fluxes to balance H^+ influx across the thylakoid membrane	Brouquisse et al. (1989)
	ATPase activity decreased	Ye et al. (2017)
	Efficiency of excitation transfer decreased	Weng et al. (2007)
	Imbalance of ionic equilibria among Cl^-, Na^+, and K^+	Bose et al. (2017)
	Decreased channel transport efficiency	Szabò and Spetea (2017)
	Diminished proton-motive force	
Calvin and Benson cycle	Decreased CO_2 assimilation	Gerardeaux et al. (2009)
	RuBisCO activity decreased	Weng et al. (2007)
	Decreased export of photoassimilates	Hafsi et al. (2014) and Hu et al. (2017)
	Impaired partitioning of assimilates	Hafsi et al. (2017) and Zahoor et al. (2017)
	Sucrose biosynthesis decreased	Hu et al. (2017)

out that the photosynthesis rate is primarily limited by biochemical process such as maximum carboxylation rate of RuBisCO and the maximum rate of electron transport rather than mesophyll and stomata conductance in K-deficient *Carya cathayensis* Sarg. In both cases, K deficiency exerts negative effects on the metabolic phases of photosynthesis, such as the Hill reaction and the Calvin and Benson cycle (Table 8.1).

8.3.2.1 Potassium Deficiency and Hill Reaction

The Hill reaction (the photochemical oxidation of water with evolution of oxygen in the presence of a suitable electron acceptor) influences the activity of both photosystems (PSI and PSII) in the chloroplasts (Dicks 1974). The nutrient deficiencies, such as those of Mn, Ca, or K, may cause a decrease in the Hill reaction activity per unit of chlorophyll as shown in isolated chloroplasts of *Solanum lycopersicum* (Spencer and Possingham 1960). Furthermore, K deficiency affects chlorophyll fluorescence by increasing thermal dissipation and reducing the efficiency of the electron transfer, efficiency of excitation transfer (Fv´/Fm´), and photochemical quenching (Spencer and Possingham 1960; Weng et al. 2007). A reduction in the efficiency of electron transfer decreases the reduction power (NADPH and ATP) and thereby affects the Calvin cycle. Studies in barley (*Hordeum vulgare*) under K deficiency pointed out a decrease in ATPase activity, with the response varying for different genotypes (Ye et al. 2017).

The homeostatic role of K in photosynthetic apparatus is relevant, especially under abiotic stress, because the ionic equilibria among Cl^-, Na^+, and K^+ to maintain the photosynthesis are dependent on K. Potassium importance is related to ion channel activity and ions transported across thylakoid stroma membranes, contributing strongly to proton-motive force and thus to photosynthetic efficiency (Bose et al. 2017; Szabò and Spetea 2017) (Table 8.1).

8.3.2.2 Potassium Deficiency Effects on Carbon Fixation in the Calvin and Benson Cycle

Several environmental stresses generate an increase in K demand to maintain CO_2 fixation in photosynthesis, but such stresses also induce an increase in ROS production. In this context, an increase in K supply may ameliorate these stresses, at least partly (Foyer et al. 1994; Cakmak 2005). Gerardeaux et al. (2009) pointed out that a deleterious effect of K deficiency on CO_2 assimilation occurred 50 days after emergence of *Gossypium hirsutum* L., concomitant with an increase in light intensity. Photosynthesis by K-starved plants at up to 2000 μmol CO_2 m^{-2} s^{-1} showed a reduction in CO_2 assimilation that could be attributed to lower response of stomata to the environmental conditions. Another possible explanation may also be a decrease in the RuBisCo activity under K deficiency (Weng et al. 2007). Although these effects varied in the several species studied, the principles are likely to be applicable across a wide range of conditions.

The adverse effects of K deficiency on photosynthetic parameters, especially CO_2 fixation, are caused by decreased leaf K concentration (7–8 g kg^{-1}) in *Carya cathayensis*, although an extent of that decrease may vary among plant species (Jin et al. 2011). In addition, Terry and Ulrich (1973) pointed out that under K starvation, the CO_2 assimilation in *Beta vulgaris* L. per unit area decreased linearly over time (i.e., with severity of K deficiency).

Potassium deficiency alters not only the photosynthetic process but also sugar metabolism and export because K is involved in the long-distance transport in plants; hence, photoassimilates, especially sugars, accumulate, and they are not converted to starch (Hermans et al. 2006; Hafsi et al. 2014; Hu et al. 2017). Nevertheless, Nikinmaa et al. (2013) pointed out that this phenomenon is also related to stomatal activity that may restrict the Calvin and Benson cycle, limiting sucrose biosynthesis and nitrate assimilation (Hu et al. 2017).

Low K supply to *Beta vulgaris* L. did not have any effect on sugar (carbon) transport in a short term (6–8 h) (Conti and Geiger 1982), suggesting that carbon mobilization in phloem is a result of the magnitude of CO_2 fixation rather than immobilization of sugar. A K deficiency effect on partitioning of assimilates is exacerbated under abiotic stresses, such as drought; moreover, K deficiency decreases net photosynthesis, transpiration and stomatal conductance, and finally biomass production (Hafsi et al. 2017; Zahoor et al. 2017) (Table 8.1).

8.4 Conclusions and Future Perspectives

Under abiotic stresses such as salinity, cold, or drought, adequate levels of K supply may contribute to stress amelioration and resistance linked to maintaining metabolic processes and plant yield. Nevertheless, more studies are required to elucidate the mechanisms involved in resistance to plant stress and how increased K supply can improve plant growth and yield.

In photosynthesis, K plays important roles in the Hill reaction as well as the Calvin and Benson cycle. In the Hill reaction, the main role is associated with generation of NADPH and ATP, where ionic equilibria, electron transport, and proton-motive force are the main processes in which K participates. In the Calvin and Benson cycle, a decrease in CO_2 fixation and sugar production and transport is associated with altered partitioning of photoassimilate, all influenced by K supply. The underlying mechanism associated with the role of K in the photosynthetic processes is poorly understood. In particular, limited sugar biosynthesis, transport, and distribution under K deficiency are important causes of photosynthetic limitations and thus poor growth and development.

It remains unclear how different photosynthetic processes respond to resupply of K and in which time frame. For example, does CO_2 fixation or carbon export and partitioning respond first? For a deep understanding of this phenomenon, more studies are necessary at the molecular level to elucidate mechanisms and regulatory point of the complex network of biochemical relationships that underlie on the photosynthetic effects under potassium deficiency.

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Chapter 9

Heavy Metal Tolerance in Two Algerian Saltbushes: A Review on Plant Responses to Cadmium and Role of Calcium in Its Mitigation

Bouzid Nedjimi

Abstract Heavy metal pollution is a common environmental constraint to human health. The physicochemical decontamination constitutes a high costly procedure and not practicable in extensive polluted soils. Therefore, selecting plants naturally tolerant to heavy metals is an alternative approach for a sustainable phytoremediation. The aptitude of species to tolerate heavy metals is determined by several biochemical trails that protect photosynthetic apparatus and maintain growth and chemical elements homeostasis. Cadmium (Cd) is a high toxic environmental pollutant and can interfere with various metabolic processes such as photosynthesis, respiration, and mineral uptake and some enzymatic activities that are crucial for plant growth. *Atriplex halimus* L. and *A. nummularia* L. (Amaranthaceae) are two widespread saltbushes used for desalination and rehabilitation of Algerian saline lands. These shrubs have a high biomass production, extensive root system, low nutrient requirements, and easy propagation, among other benefits. Calcium (Ca) supplementation was largely used to improve heavy metal tolerance of plant species. Ca is an indispensable element for plant growth, membrane integrity, osmotic adjustment, and signaling transduction. Exogenous application of this element can play a significant role to enhance plant tolerance against Cd toxicity. This chapter reviews the tolerance of *A. halimus* and *A. nummularia* saltbushes to Cd stress and the impact of this heavy metal on physiological and biochemical traits. In addition the beneficial role of Ca supplementation to alleviating Cd toxicity in these species was discussed.

Keywords *Atriplex* sp. · Cadmium toxicity · Calcium addition · Halophytes · Heavy metals · Phytoextraction · Phytostabilization · Pollution

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9.1 Introduction

Halophytic species can propagate and uptake toxins and pollutants (salts and heavy metals) in nonconventional soils (saline and polluted sites) to the amount that many glycophyte species cannot (Hasanuzzaman et al. 2014). These plants have involved well-adapted morphological and physiological features that enable them to tolerate high heavy metal pollution. Exploitation of these plants for rehabilitation of contaminated soils can be a promising strategy for sustainable phytoremediation (Manousaki and Kalogeraki 2011). However, it is essential to identify the strategies that these species applied to protect themselves and complete their life cycle under high polluted conditions (Lutts and Lefèvre 2015).

Cadmium (Cd) is a nonessential heavy metal that disrupts many physiological activities and prevents plant growth and development (Nedjimi and Daoud 2009; Hasanuzzaman and Fujita 2012). It is known as an extremely pollutant metal due to its toxicity and high solubility in soil solution (Sanitá di Toppi and Gabbrielli 1999). The main causes of soil pollution by Cd are the industrial and mining activities, use of phosphate fertilizers, and utilization of slug water for agriculture irrigation (Kabata–Pendias 2004).

The contamination of soil by Cd is one of the gravest environmental problems and has substantial consequences for human health. The noticeable symptoms of Cd toxicity in plants comprise (i) leaf chlorosis (chlorophyll breakdown), (ii) growth retardation, (iii) inhibition of enzymatic reactions, (iv) mineral nutrition disturbance, (v) lipid peroxidation, and (vi) production of reactive oxygen species (ROS) (Das et al. 1997; Hasanuzzaman et al. 2017a, b).

The use of classical methods such as soil excavation, chemical precipitation, electroplating, and incineration for heavy metal decontamination was quite costly and may induce to soil degradation. However phytoremediation, based on the use of plant species to eliminate contaminants, has been applied as a promising, no impact in environment, and low-costly green technology (Wu et al. 2010).

Solís-Domínguez et al. (2007) proposed that the normal content of Cd in leaf tissue ranges 0.05–0.2 μg g^{-1} DW, and 5–10 up to 30 μg g^{-1} DW can be considered excessive or toxic. However, Cd hyperaccumulator species accumulate above 100 mg μg g^{-1} DW.

The criteria to categorize plants as Cd-tolerant or hyperaccumulator species are (i) species which prevent the Cd assimilation in shoots by retaining Cd in their roots (type *excluder*), (ii) species which accumulate Cd in their shoots through production of chelators or sequestration of Cd in nonsensitive compartments of vacuoles (type *includer*), and (iii) species which concentrate Cd in their shoots to levels far above than in soil (hyperaccumulators) (Maestri et al. 2010).

Heavy metal phytostabilization is a method used to reduce the bioavailability and migration of metals and stabilize them in the rhizospheric system and/or accumulated in root tissue. Phytoextraction is a technique to extract metals by plant from soils and accumulated them in aboveground harvestable parts (Susarla et al. 2002).

Saltbushes are a robust xero-halophyte species that are capable to survive with extensive periods of drought with high salinity and heavy metal levels (Nedjimi and Daoud 2009; Nedjimi et al. 2013; Barakat et al. 2013).

Among the halophytic species, *Atriplex* spp. are important shrubs of the Amaranthaceae family. These saltbushes have a distinct biochemical and physiological plasticity that permits them to survive under harsh circumstances including drought, salinity, and heavy metal pollution (Le Houérou 1992).

Dotted with high aboveground biomass accompanied by a profound root system, many species of the genus *Atriplex* were tested for their potential as suitable candidates for phytoremediation and cleanup of heavy metals from contaminated soils (Sawalha et al. 2006; Lomonte et al. 2010; Vromman et al. 2011; Saïdani and Nedjimi 2014).

Atriplex halimus L. (Mediterranean saltbush, Fig. 9.1a) is a perennial shrub widespread throughout the West Asia and North Africa areas (WANA) and is used widely to provide fodder to livestock, due to its drought and salinity tolerance and its high palatability (Le Houérou 1992); however, *A. nummularia* L. (old man saltbush, Fig. 9.1b) is a halophytic shrub that naturally occurs in the Australian dry lands and is frequently used to stabilize sandy soils (Silveira et al. 2009).

The results of hydroponic experiments performed with *A. halimus* grown with increasing concentrations of Cd revealed that the main Cd content was accumulated in root system, and the Cd contents in shoot part remained particularly at small levels indicating a significant restriction of the translocation of Cd from the roots to aboveground part. In addition, all plants remained alive until the end of the experiment, and no visible toxicity symptoms were shown in plant treated with low doses of Cd (Nedjimi and Daoud 2009).

The main objective of the this chapter is to provide a comprehensive review of the major responses of two *Atriplex* species to Cd and the mechanism adaptation of these species against Cd stress by calcium supplementation.

Fig. 9.1 The *Atriplex* species (Amaranthaceae): *A. halimus* (**a**) and *A. nummularia* (**b**)

9.2 Cadmium Effects on Seed Germination

Seed germinability and early seedling growth are the most important stages in the life cycle of plants that determine their propagation and establishment in field conditions (Nedjimi et al. 2014).

Metal stress may decrease seed germinability by delaying germination, enhancing of seed mortality, decreasing activities of some enzyme involved in germination events, and prolonging the seed dormancy (Sethy and Ghosh 2013).

The main physiological syndromes shown during seed germination under metal stress are (i) a decreased of seed imbibition, (ii) perturbation of reserve hydrolysis, and (iii) alteration activities of enzymes (Wierzbicka and Obidzinska 1998; Ashraf et al. 2011).

The aptitude of plant to tolerate Cd toxicity depends upon its ability to germinate in Cd-polluted soils (Márquez-García et al. 2013). *Atriplex halimus* and *A. nummularia* seeds showed the highest percentage of germination without Cd stress (control treatment). However germination was inhibited when $CdCl_2$ concentrations increased in the medium. At high $CdCl_2$ (200 μM) concentration, about 40% and 70% of the seeds germinated, respectively, for *A. nummularia* and *A. halimus* (Fig. 9.2).This suggests that *A. halimus* was a more Cd-tolerant saltbush compared to *A. nummularia.*

In another halophyte shrub, Liu et al. (2012) showed that final germination percentage of *Suaeda salsa* was prevented with the increased of $CdCl_2$ concentrations. Cd inhibited seed germination significantly from 88% to 18% at 6 mg L^{-1} $CdCl_2$. Seed germination of *Miscanthus floridulus* and *M. transmorrisonensis* was reduced to 3% and 8%, respectively, at 200 μM Cd treatment (Hsu and Chou 1992). A high

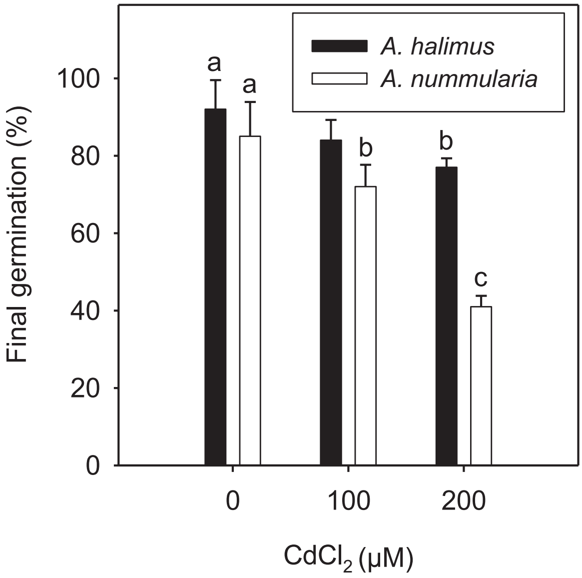

Fig. 9.2 Effect of $CdCl_2$ on final germination percentages of two *Atriplex* species. Bars represent mean ± SE ($n = 4$). Different letters above bars indicate significant difference at $P < 0.01$ according to *Tukey*'s multiple range test

concentration of Cd (400 μM) inhibits significantly seed germination and early growth of *Brassica napus* compared to control (Meng et al. 2009). Aydinalp and Marinova (2009) demonstrated that concentration of 40 ppm $Cd(NO_3)_2$ repressed significantly seed germination and seedling growth of *Medicago sativa* grown in solid media (agar substrate).

9.3 Cadmium Effects on Biomass Production

Growth inhibition and reduction of the biomass production are mainly remarkable symptoms of Cd toxicity (Das et al. 1997). The biomass decrease observed in plants exposed to Cd often consequences from direct effects (toxicity of Cd accumulated in tissues) and/or from indirect effects (mineral nutrition deficiencies).

Kramer (2010) defined metal tolerance as the capability of plant to complete their growth cycle under polluted conditions with rapid growth, high green biomass, and extraction of high amount of metals in their tissues, without symptoms of toxicity.

The roots display rapid and sensitive modifications in their growth pattern due its direct contact with toxic elements by reduction of root elongation and hair density and enhancement of lignification (Clemens 2006).

Both shoot and root dry weights (DWs) of *A. halimus* and *A. nummularia* have shown a significant reduction with an increase in Cd treatment (Fig. 9.2). Analogous findings have been reported for other saltbush species such as *Spartina alterniflora* (Chai et al. 2013) and *Suaeda fruticosa* (Bankaji et al. 2015) subjected to Cd stress. Li et al. (2016) revealed that application of 50 μM Cd in nutrient solution significantly repressed the dry weight accumulation and enhanced the content of hydrogen peroxide (H_2O_2) and lipid peroxidation in *Arabidopsis* seedling. After 1 month of treatment, addition of Cd (50–300 μM $CdCl_2$) in the medium culture decreased the relative growth rate of halophytes *Sesuvium portulacastrum* and *Mesembryanthemum crystallinum* (Ghnaya et al. 2005). The same authors proposed nutrient amendments (especially Ca and K) to improve plant growth and Cd phytoextraction of both halophytes.

9.4 Cadmium Effects on Photosynthesis Apparatus

Cadmium decreases photosynthesis of plants by many factors such as chloroplast alteration (Ouzonidou et al. 1997), enhancement of senescence (Prakash et al. 2003), perturbation of enzymatic activity, and reduction of stomatal conductance by limiting the CO_2 rates for carboxylation (Bertrand and Poirier 2005). Küpper et al. (1998) suggested that Cd substituted Mg in chlorophyll and led to alteration of chlorophyll pigments.

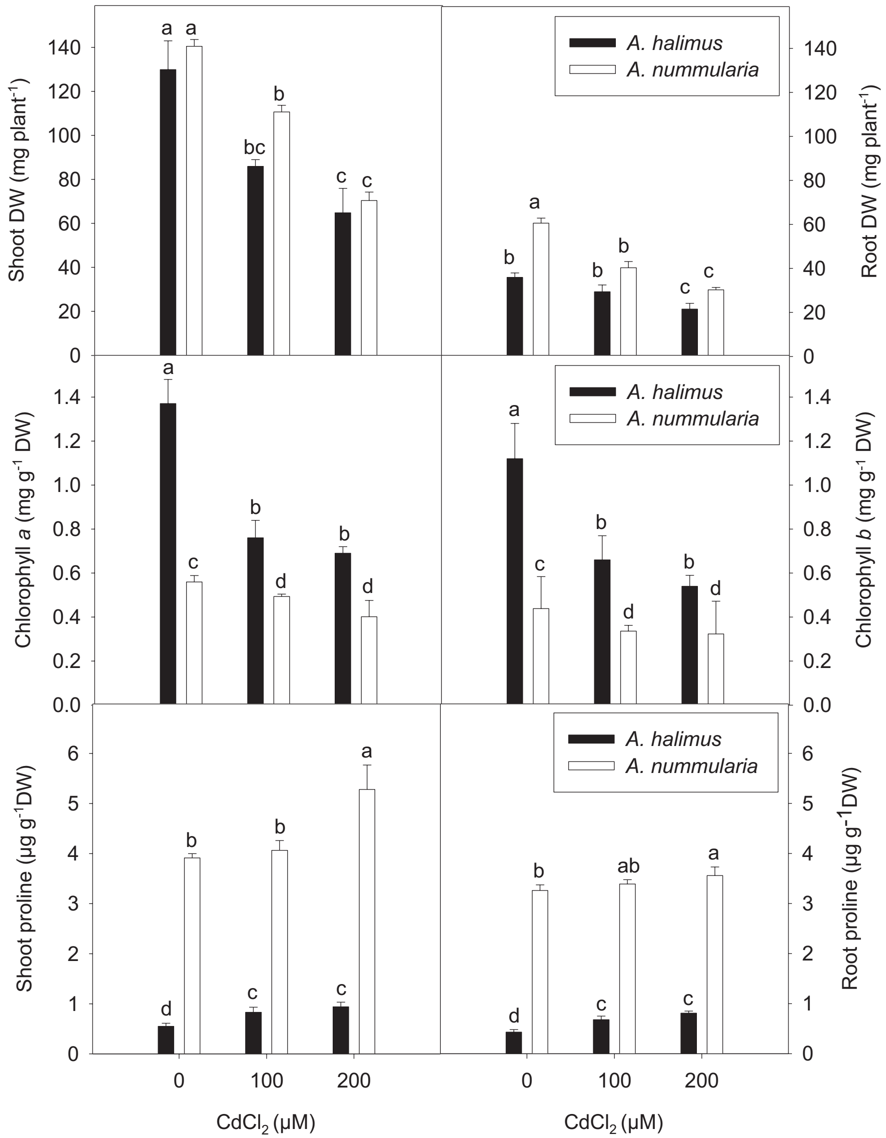

Fig. 9.3 Effect of $CdCl_2$ on dry weights (DW), chlorophylls (**a**, **b**), and proline content of two *Atriplex* species. Bars represent means ± SE ($n = 5$). Different letters above bars indicate significant difference at $P < 0.05$ according to *Tukey*'s multiple range test

The effect of Cd on photosynthesis in higher plants is extensively studied. Thus, in our previous studies, Cd stress reduces significantly chlorophyll contents (Chl *a* and *b*) in both *Atriplex* species (Fig. 9.3). A significant decrease in contents of chlorophyll and carotenoid was established in *Myriophyllum spicatum* and *M. triphyllum* under the Cd application (Sivaci et al. 2004). Likewise, Deng et al. (2014) observed photo-inhibition and low electron transport rate in the leaves of *Ceratopteris pteridoides* due to Cd toxicity. Dias et al. (2012) demonstrated that application of 10 and 50 μM Cd in nutrient solution can decrease the net CO_2 assimilation rate and the photosystem II efficiency of lettuce. In addition, Cd perturbed photosynthesis activity in halophyte green alga (*Chlamydomonas reinhardtii*) by inhibiting photoactivation of photosystem II and preventing CO_2 fixation (Faller et al. 2005).

9.5 Cadmium Effects on Mineral Uptake

The progressive concentrations of $CdCl_2$ contribute to increased Cd contents in *A. halimus* which was found to be higher in the roots (508.17 μg g^{-1}DW after 15 days at 200 μM $CdCl_2$) than in the shoots. However, the inverse findings were found in *A. nummularia* where the highest Cd contents occurred in the shoots (146.59 μg g^{-1} DW after 15 days at 200 μM $CdCl_2$) than in the roots (Fig. 9.4). At high $CdCl_2$ (200 μM) concentration, the accumulation of Cd in *A. halimus* was reported to be five times higher in the roots than in the shoots. However in *A. nummularia* Cd content was found to be two times higher in the shoots than in the roots. These findings suggest that *A. nummularia* could be a suitable shrub for Cd phytoextraction; however, *A. halimus* could be appropriate for use in the phytostabilization of Cd in polluted soils.

Many strategies were suggested to elucidate the ability of roots to accumulate high amounts of Cd; among these are (i) Cd complexation by organic acids such malate and oxalate (Lutts et al. 2004), (ii) Cd sequestration by phytochelatins (PCs) (Stolt et al. 2003), and (iii) Cd compartmentation in vacuoles (Shevyakova et al. 2003).

Many plant species retained high contents of Cd in their roots, with reduced translocation of this metal to aboveground part, or retransferred Cd from shoots to roots through the phloem path (Schmidke and Stephan 1995). However, substantial hypothesis suggested for Cd translocation to shoots was founded principally by water flux due to transpiration and root pressure (Zhao et al. 2006).

The halophyte *Avicennia marina* possesses the ability to accumulate Cd via its root system and stock in shoots without any sign of toxicity and suggests as a phytoextraction halophytic species (Nirmal Kumar et al. 2011). Recently, Eissa (2015) found that *Atriplex lentiformis* and *A. undulate* were appropriate halophytic shrubs for Cd phytostabilization and can reduce Cd contents in their aerial parts when the soil was contaminated by high Cd concentration. The salt marsh halophyte *Sesuvium portulacastrum* easily accumulates Cd from tannery effluent making it a viable candidate for use in phytoextraction in salt marshes (Ayyappan et al. 2016).

Cd toxicity may consequence from disruption in plant metabolism activities as a result of disorder in the mineral uptake by root and translocation to aboveground part (Das et al. 1997).

Potassium (K) is a vital chemical element involved in protein genesis, photosynthetic activity, enzyme stimulation, and cell osmotic adjustment (Maathuis and Amtmann 1999). The capacity of plants to avoid Cd stress depends strongly on the

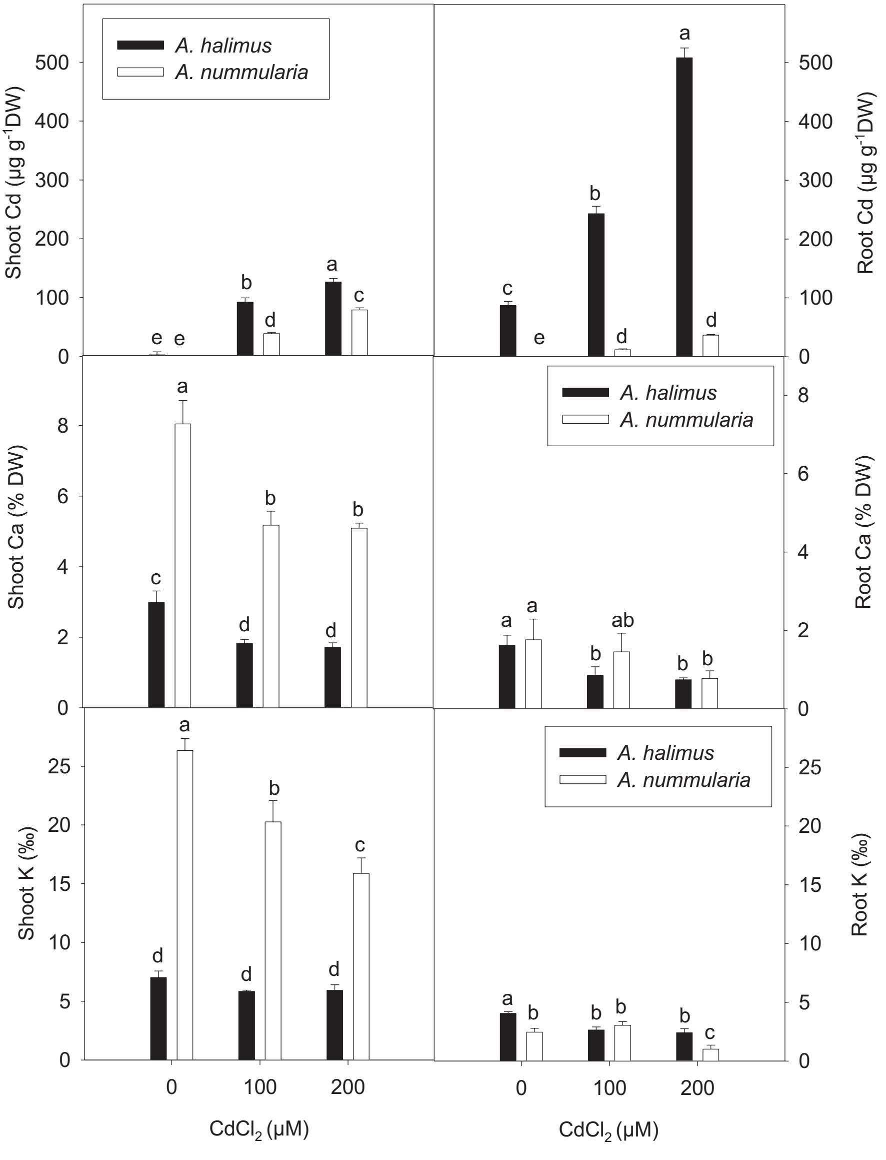

Fig. 9.4 Effect of $CdCl_2$ on cadmium (Cd), calcium (Ca), and potassium (K) contents of two *Atriplex* species. Bars represent mean ± SE ($n = 5$). Different letters *above bars* indicate significant difference at $P < 0.05$ according to *Tukey*'s multiple range test

status of their K absorption. The increase of external $CdCl_2$ concentration was accompanied by a simultaneous decrease in K contents. Cd can reduce the root uptake of K and product K deficiency and growth retardation (Ghnaya et al. 2007).

Little information exists about the direct effect on uptake and distribution of K in plant subject to Cd stress. Cd and K possess a different chemical similarity; thus Cd plays an indirect influence on K uptake, probably by decreasing energy disposability through ATP complexation (Asp et al. 1994) or by depressing the genes implicated in the transport of K influx (Ahmad and Maathuis 2014). Under high Cd stress, K assimilation was altered by the uncontrolled influx of Cd through the K pathways. Accumulation of Cd and its sequestration into the vacuole subsequently limit the K uptake by roots and decrease their translocation to the shoots (Das et al. 1997). K concentrations in shoots and roots of both *Atriplex* spp. decreased significantly with an increase of Cd level (Fig. 9.4). Similarly, a dramatic inhibition of K absorption was observed in *Mesembryanthemum crystallinum* cultivated on nutrient solution supplemented with $CdCl_2$ (Ghnaya et al. 2005).

Our results show that Cd in the medium culture decreases calcium (Ca) contents in different plant organs of both saltbushes (Fig. 9.4). Reduction of growth related to a disturbance of Ca assimilation induced by Cd has been shown in many halophytic species such as *Sesuvium portulacastrum* and *Mesembryanthemum crystallinum* (Ghnaya et al. 2007). Clemens (2006) indicated that Cd ions competed (antagonist) for the same channels or transporters with Ca cation in root cell membrane. Wang and Song (2009) establish that application of 5 mM $CaCl_2$ in the nutrient solution can significantly contract the toxicity of Cd in *Trifolium repens*, by alleviating lipid peroxidation and promoting activity of antioxidative enzymes. In *Arabidopsis* seedlings, Suzuki (2005) found that Cd contents were decreased by supplementation of 30 mM Ca.

9.6 Cadmium Effects on Organic Solute Accumulation

Under metal stress, plants accumulate large amounts of compatible solutes such as proline, glycine betaine, and soluble sugars. These metabolites defend cells from oxidative damage produced by free radicals (ROS) and maintain the normal enzymatic activities without inhibition of the cellular metabolism (Ashraf and Foolad 2007). Metals are habitually compartmentalized in the vacuoles, while organic solutes are sequestered in the cytosol to protect cell from metal toxicities (Zouaria et al. 2016).

Proline is the most commonly compatible osmolyte accumulated by plants under abiotic stresses. This metabolite is involved in osmoregulation, carbon storage, radical scavenging, and stabilization of the structure of proteins such as RuBisCO (Nedjimi 2013). The ability of halophytic species to synthesize this organic compatible solute may be involved in their aptitude to cope with heavy metal stress (Sharma and Dietz 2006).

Atriplex halimus and *A. nummularia* accumulate large quantities of proline that often contributes to maintain its growth potentialities when exposed to Cd stress (Fig. 9.3). In another study, proline content was enhanced at high concentrations of Cd (300 µM $CdCl_2.H_2O$) in the extreme halophyte *Salicornia brachiata*, which is capable of accumulating this heavy metal in their areal part (Sharma et al. 2010). Likewise, Shevyakova et al. (2003) revealed that the exposition of *Mesembryanthemum crystallinum* plants which is a facultative halophyte, to excess Cd doses (0.01–1 mM), produced a general increase in proline accumulation. A significant increase of proline contents was also established in *Silene vulgaris* under the Cd application (Schat et al. 1997). In halophyte *Aeluropus littoralis*, the concentration of proline increased with increased concentrations of heavy metals (Cd, Co, Pb, and Ag) in nutrient solution (Rastgoo and Alemzadeh 2011). Measurement of proline content showed the existence of positive and linear correlation between proline contents and Cd concentrations in *Triticosecale* Wittmack seedling treated with cadmium nitrate (Talebi et al. 2014).

9.7 Calcium Application Mitigates Cadmium Toxicity

Calcium is an essential element in many cellular functions, including enzyme activation, membrane integrity, and signal transduction (White and Broadley 2003). Soil pH or soil acidity (related to Ca level in the soil) was considered as the chemical factor that affects directly the solubility and bioavailability of Cd in soil rhizosphere. Many reports indicated that the reducing of pH of soil solution leads to reducing Cd solubility and uptake by plants (Kirkham 2006).

In field conditions, adequate supplementation of Ca in polluted soils is a suitable low-cost solution to monitoring heavy metal toxicities, particularly in plant species which are subjected to Cd contamination (El-Enany 1995). The exogenous addition of Ca during the earlier growth stage can help plants to escape toxicity upon exposure to Cd and offer a promising strategy to improve crop tolerance against Cd with minor damages as possible (Huang et al. 2017).

It is well-known that addition of exogenous Ca in nutrient solution alleviates the deleterious effects of Cd stress by inhibiting the uptake of Cd and repairing of membrane leakage and antioxidant system (Wang and Song 2009; Nedjimi 2009). The presence of Ca in soil solution can prevent Cd uptake by roots (Lux et al. 2011). This cation can affect Cd assimilation as a consequence of antagonism in specific channels of ion transport. This suggestion was largely sustained by the study of Li et al. (2012) who revealed that application of lanthanum chloride ($LaCl_3$) (Ca channel blocker) can significantly reduce Cd penetration in roots of *Suaeda salsa*.

Exogenous application of Ca can prevent adverse impact of Cd in cell membranes and decrease the leakage of cytosolic K. In this way it may restore the K status that is altered by Cd stress. For example, Nedjimi (2009) found that supplementation of 20 and 40 mM $CaCl_2$ alleviates adverse effects on the growth of *A. halimus* plants. This promoting effect of Ca on growth was associated with increase in K, Ca, and Fe deficiencies joined with decrease in Cd content (Table 9.1). Similarly, Zhenyan et al. (2005) demonstrated that the growth enhancement effect of supplemental Ca on *Lactuca sativa* was due to the improvement of phytochelatin synthase gene expression. Recently Hashem et al. (2017) found that application of Ca associated with the arbuscular mycorrhizal fungi inoculation produced a significant decrease in lipid peroxidation and hydrogen peroxidation and strengthened the antioxidant system of *Bassia indica* seedlings.

Table 9.1 Effect of calcium supplementation (20 and 40 mM) on dry weights (DW), chlorophyll contents (*a* and *b*), and cadmium (Cd), calcium (Ca), and iron (Fe) concentrations in shoot and root of *A. halimus* grown in nutrient solution containing high concentration of $CdCl_2$ (400 µM)

	DW (mg plant^{-1})		Chlorophyll (mg g^{-1} DW)		Cd (µg g^{-1}DW)		Ca (% DW)		Fe (µg g^{-1}DW)	
Treatments	Shoot	Root	Chl *a*	Chl *b*	Shoot	Root	Shoot	Root	Shoot	Root
Control	127.9 a	37.7 a	1.74 a	1.13 a	1.22 c	2.31 c	2.83 a	1.62 a	13.13 a	121.75 a
$CdCl_2$	56.5 c	18.2 c	0.64 b	0.43 c	209.51 a	618.23 a	0.97 c	0.57 c	6.03 c	38.66 c
$CdCl_2$ + 20 Ca	79.9 b	23.8 b	0.95 ab	0.76 b	175.42 b	572.12 b	1.11 b	0.95 b	8.67 ab	74.12 b
$CdCl_2$ + 40 Ca	86.6 b	28.1 b	1.09 a	0.91 b	109.63 b	507.23 b	1.93 ab	1.06 b	10.45 b	84.34 b

Different letters in the same column indicate significant difference at $P < 0.05$ according to *Tukey*'s multiple range test

The protective character of Ca in the Cd stress shown in *Trifolium repens* seedlings was associated with growth improvement and enhancement of some antioxidative enzymes such as glutathione peroxidase (GPOX) and catalase (CAT) (Wang and Song 2009). A hydroponic experiment with *Sedum alfredii* was conducted by Tian et al. (2011) to investigate the ameliorating effect of Ca on root growth and oxidative stress caused by Cd. Their results showed that addition of Ca to the nutrient solution mitigates Cd toxicity by a significant increase in the plasma membrane integrity and glutathione (GSH) biosynthesis.

Wheat LCT1, a nonspecific transporter for Ca and Cd, was overexpressed in tobacco plants. LCT1-transformed plants treated with 0.05 mM $Cd(NO_3)_2$ and 1 mM $Ca(NO_3)_2$ displayed a substantially higher level of tolerance to Cd (Antosiewicz and Hennig 2004). Likewise, Drążkiewicz and Baszyński (2008) revealed that supply of 10 mM Ca to nutrient solution can help *Phaseolus coccineus* L. cv. Piękny Jaśto maintain protein composition of PS II complex and chlorophyll *a* fluorescence caused by the presence of 250–1000 µM Cd.

El-Enany (1995) reported that Ca supply significantly counteracted the harmful effect of Cd in maize seedlings. This was related to reduction of Cd accumulation and stimulation of biosynthesis of pigments and respiration rate. Contrary, Huebert and Shay (1991) showed that additional Ca to *Lemna trisulca* seedlings had no significant impact on Cd toxicity with regard to growth rate, final yield, and cadmium uptake. Shi et al. (2014) suggested that supplemental Ca had a mitigating effect on Cd-induced cytotoxicity by efficiently improving the mitotic index and reducing the rate of chromosomal aberration in root of *Wedelia trilobata*. Li et al. (2016) revealed that application of 3 mM Ca in the nutrient solution can alleviate the root growth inhibition and reduce oxidative damages caused by Cd through maintaining auxin homeostasis in *Arabidopsis* seedlings.

The protective effect of $Ca(NO_3)_2$ against Cd toxicity in *Lens culinaris* cultivated in Hoagland nutrient could be attributed to the decrease of the levels of H_2O_2 and protection of membrane integrity (Talukdar 2012). Sakouhi et al. (2016) showed that addition of exogenous Ca together with ethylene glycol tetraacetic acid (EGTA) in the nutrient solution mitigated the growth inhibition and decreased lipid peroxidation and protein carbonylation in both shoot and root of *Cicer arietinum* plants exposed to Cd stress. In hydroponic condition, Farzadfar et al. (2013) showed that addition of 0.1, 1, and 5 mM $CaCl_2$ decreased the Cd content and reactive oxygen species accumulation in *Matricaria chamomilla* seedlings treated with 120 and 180 µM $CdCl_2$.

9.8 Conclusion and Perspectives

Cadmium is a highly toxic heavy metal that induces damages in plants at physiological, metabolic, and biochemical processes. Many halophytic species can tolerate high amount of Cd and even accumulate Cd in their organs, therefore emphasizing their potential for phytoremediation of Cd-contaminated soils.

The present review analyzes research undertaken during the last decade to understand the tolerance mechanism in two *Atriplex* saltbushes to Cd stress. In arid zones of Algeria, *A. halimus* and *A. nummularia* (Amaranthaceae) are the two dominant saltbushes used as a fodder for livestock, for revegetation to preserve soil against desertification, and for desalination and phytoremediation of the polluted soils. These shrubs tolerate abiotic stress such as salinity, drought, and heavy metals. *A. halimus* was found to be accumulating a higher content of Cd in the roots. However, in *A. nummularia*, most of the Cd taken up was retained in shoots. These findings suggest that *A. nummularia* could be a suitable shrub for phytoextraction; however, *A. halimus* could be more appropriate for use in the phytostabilization of Cd in polluted soils. These saltbushes have the capacity to develop in the Cd-polluted soils and accumulate large amounts of Cd in their tissues. However exogenous Ca amendments can be supplemented to enhance the phytoremediation efficiency and to help saltbushes to cope better with Cd toxicity. The appropriate dose and duration of treatment of the exogenous Ca application should be determined precisely. In addition, further investigations considering molecular approaches are needed to reveal the underlying mechanisms of Cd tolerance in these species.

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Chapter 10
The Role of Sulfur in Plant Abiotic Stress Tolerance: Molecular Interactions and Defense Mechanisms

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Abstract Sulfur (S) is an essential macronutrient in plants that serves numerous plant functions and is vital for the metabolic processes. Moreover, it is the constituent of some essential amino acids and metabolites. Recent studies have provided the notion that S not only improves the productivity of plants under normal condition but also protects them from abiotic stresses like salinity, drought, and toxic metals/metalloids. Different S compounds directly act as antioxidants or modulate antioxidant defense system. Among them, glutathione (GSH) is regarded as one of the powerful antioxidants and stress protectors. Interactions of S with other biological molecules afford stress signaling to provide defense against environmental stresses. However, the S uptake, translocation, and mechanisms of action in plants under stressful conditions are still under research. The recent progress on the roles of S in conferring abiotic stresses and related literature is presented in this chapter.

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Abbreviations

ABA	Abscisic acid
ACS	1-Aminocyclopropane carboxylic acid (ACC) synthase (ACS)
APK	APS kinase
APR	Adenosine-5′-phosphosulfate reductase
APS	Adenosine-5′-phosphosulfate
APX	Ascorbate peroxidase
AsA	Ascorbate
ATP	Adenosine triphosphate
ATPS	ATP sulfurylase
CAT	Catalase
CBL	Cystathionine β-lyase
CGS	Cystathionine γ-synthase
CSC	Cysteine synthase complex
Cys	Cysteine
Cyst	Cystathionine
DHA	Dehydroascorbate
DHAR	Dehydroascorbate reductase
EF-TU	Elongation factor-thermo unstable
GAPDH	Glyceraldehyde-3-P-dehydrogenase
GB	Glycine betaine
GCL	Glutamate-cysteine ligase
Gly I	Glyoxalase I
Gly II	Glyoxalase II
GPX	Glutathione peroxidase
GR	Glutathione reductase
GRX	Glutaredoxins
GSH	Glutathione
GSHS	Glutathione synthetase
GSSG	Oxidized glutathione
GST	Glutathione S-transferase
h-GSH	Homo-GSH
JA	Jasmonates
LOX	Lipoxygenase
MDA	Malondialdehyde
MDHAR	Monodehydroascorbate reductase
Met	Methionine

MG	Methylglyoxal
MRNA	Messenger ribonucleic acid
MS	Methionine synthase
NaHS	Sodium hydrosulfide
NPT	Nonprotein thiol
OAS	O-Acetylserine
OASS	O-Acetylserine sulfhydrylase
OAS-TL	OAS(thiol)lyase
OPH	O-Phosphohomoserine
PAPS	3-Phosphoadenosine-5-phosphosulfate
PCs	Phytochelatins
PEG	Polyethylene glycol
POD	Peroxidase
POX	Peroxidases
ROS	Reactive oxygen species
RT-PCR	Reverse transcription polymerase chain reaction
RuBisCO	Ribulose-1,5-bisphosphate carboxylase/oxygenase
SAT	Serine acetyltransferase
Ser	Serine
SiR	Sulfite reductase
SLG	*S*-D-Lactoylglutathione
SOD	Superoxide dismutase
SULTR	Proton/SO_4^{2-}cotransporter in plants
SURE	Sulfur-responsive element
TBARS	Thiobarbituric acid reactive substances
TRX	Thioredoxins
γ-ECS	γ-Glutamylcysteine synthetase
γ-GluCys	γ-Glutamylcysteine

10.1 Introduction

Water stress, temperature stress, salinity stress, metal stress, nutrient deficiency, UV radiation, and ozone stress are being the most common abiotic stresses throughout the world. Growth and phenological pattern and reproductive development are hampered due to obstruction in water and nutrient uptake, photosynthetic activity, mitochondrial reaction, and plasma membrane transportation of cell organelles in plants grown under abiotic stress condition (Hasanuzzaman et al. 2012, 2017a). The intensity of these stresses is increasing day by day at an alarming rate, and because of that, the abiotic stresses become a matter of immense anxiety to plant productivity. That is why research on abiotic stress effects and how to decrease abiotic stress effects on plants have been increased noticeably previously. Inherent struggling capacity for survival in the era of abiotic/biotic stresses determines the healthy growth of any organisms including plants. Naturally, like any other organisms, plants' genetic potential determines the ability to struggle and survive against abiotic stresses.

Keen observation of plant processes and biomolecules within plants has recognized sulfur (S) as one of the most abundant elements in organic structures. Sulfur is the fourth most important plant nutrient after N, P, and K. Sulfur after taken up by the root in the form of sulfate (SO_4^{2-}) integrated into cysteine (Cys). Cysteine acts as a precursor or donor of key S compounds such as methionine (Met), *S*-adenosylmethionine, glutathione (GSH), homo-GSH (h-GSH), phytochelatins (PCs), sulfolipids, iron-sulfur clusters, allyl Cys, and glucosinolates, which play role in plant developmental processes and/or stress adaptation processes (Rausch and Wachter 2005; Khan et al. 2014; Anjum et al. 2015). Glutathione and h-GSH are involved in stress signal transmission. Several key stress metabolites such as ethylene (C_2H_2) are controlled by *S*-adenosylmethionine. Sulfur compound-mediated function of ATP-S has been reported for stress tolerance response (Anjum et al. 2015). Cysteine improved growth and lessened oxidative stress by modulating cellular redox status and antioxidant defense in barley (Genisel et al. 2014). Sulfur-induced GSH synthesis decreased reactive oxygen species (ROS) and improved photosynthetic efficiency and growth in salt-affected barley (Astolfi and Zuchi 2013). Higher content of S uptake increased accumulation of proteinogenic and non-proteinogenic thiols which improved cadmium (Cd) tolerance (Sun et al. 2007; Lancilli et al. 2014). The S deficiency reduces chl (chl) content, photosystem (PS) II efficiency, and performance of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo) (Lunde et al. 2008). Sulfur moiety of Cys can regulate disulfide bond of proteins, which affect the structure of the Fe-S cluster and function of photosynthetic apparatus and electron transport chain (Rochaix 2011). Glyceraldehyde-3-P-dehydrogenase (GAPDH), malate dehydrogenase (MDH), and elongation factor-thermo unstable (EF-TU) are some Cys-bearing protein having oxidative thiol modification functions (Leichert et al. 2008). Ethephon and N jointly augmented S-mediated ethylene and diminished glucose sensitivity, thus improving photosynthesis and growth (Iqbal et al. 2011).

Sulfur has been reported to improve antioxidant defense and metal chelation under Cd stress. In the presence of S, the GSH content, ratio of GSH and glutathione disulfide, GSSG (GSH/GSSG), nonprotein thiols (NPTs) and PCs, ascorbate (AsA) content, ratio of AsA and dehydroascorbate, DHA (AsA/DHA), activities of ascorbate peroxidase (APX), glutathione reductase (GR), and catalase (CAT) improved in Cd-affected Indian mustard plant. Moreover, superoxide dismutase (SOD) expression was upregulated that decreased $O_2^{\bullet-}$ (Bashir et al. 2015). Sulfur addition decreased the As uptake and content in the shoot and modulated thiol metabolism, glycolysis, and amino acid in rice (Dixit et al. 2015a). Thus, S is proved as a potent plant nutrient for plant developmental processes.

There are some sporadic researches on the effect of S on abiotic stress alleviation in plants. Few research findings said about signaling function of S and its derivatives. Based on available research findings, it is obvious that S is a potent molecule that functions in plant developmental and abiotic stress adaptation processes. It is necessary to extend research with S to exploit its function thoroughly. So, a comprehensive review presenting available information and research updates of S will be a base for filling up gaps of previous or existing researchers and exploring new research areas. Therefore, this review concentrates and gathers information on various aspects of S in plants including S metabolism, biological roles and roles in abiotic stress condition of S and its derivatives in plants, and molecular approaches in regulating S status.

10.2 Biological Role of Sulfur in Plants

Plants require a right combination of nutrients to survive, grow up, and reproduce. Sulfur is considered as an indispensable plant macronutrient required by all crops for their normal growth and development (Fig. 10.1). Sulfur is uptaken from the soil solution by the plant principally in the form of SO_4^{2-} (Davidian and Kopriva 2010; Capaldi et al. 2015). Moreover, different S-containing amino acids provide S to the plants. Very little amount of S is supplied from the atmospheric SO_2 and hydrogen sulfide (H_2S) where SO_2 is absorbed by leaf and fruit of plant (Mazid et al. 2011), and H_2S is absorbed through stomata of the leaf (Riemenschneider et al. 2005). Sulfur has an immense function in fundamental processes of plants such as electron transport, cellular structure, and regulation of different metabolic pathways (Capaldi et al. 2015). Sufficient S nourishment to the plants improves photosynthesis by increasing chl formation and contributes to growth and development of plants (Scherer 2008). Furthermore, it has insightful relation with N assimilation. Carciochi et al. (2017) reported that optimum S in the growing media of wheat (Z51) increased nitrogen uptake and improved the root growth, which played a central role in improving yield (Salvagiotti et al. 2009). Sulfur is also a component of various amino acids (Cys, Met etc.), antioxidants, sulfolipids, proteins, and enzymes that

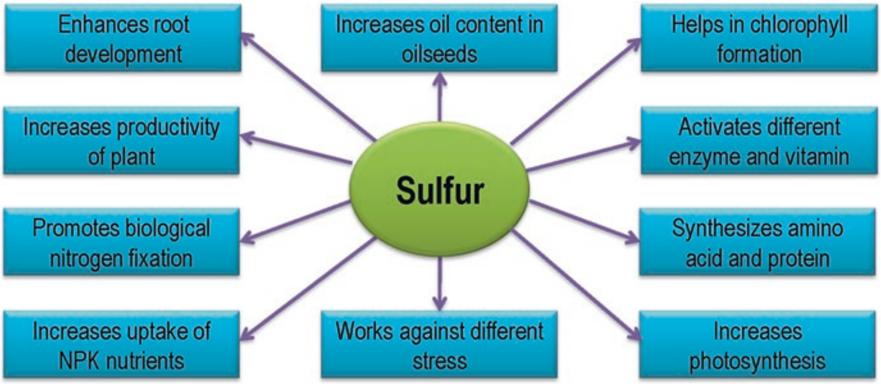

Fig. 10.1 Different biological functions of S in plants

regulate photosynthesis and biological nitrogen fixation and assimilation by the plant (Abdallah et al. 2010; Capaldi et al. 2015). Also, S is an important constituent of Fe-S clusters, lipids, polysaccharides, and a wide range of biomolecules, for instance, vitamins, cofactors, peptides, and different secondary products (allyl cysteine sulfoxides, glucosinolates, etc.) (Nocito et al. 2007; Iqbal et al. 2012). Sulfur is essential for the vegetative development and production of oil and proteins of the plant especially in oilseed crops (D'Hooghe et al. 2013; Mária et al. 2017). Many reports demonstrated the influential effect of S on the yield and total oil content of oilseed crops (Jankowski et al. 2008; Egesel et al. 2009). Sulfur is also responsible for the production of glucosinolates in both the vegetative parts and the seed of oilseed crops, which determine the pungency of plants (Walker and Booth 2003). Sulfur is known to interact with almost all essential macro- and micronutrients by influencing their uptake and utilization (Abdin et al. 2003).

Besides playing an imperative role in growth, development, and productivity of higher plants, S has an immense role to develop stress tolerance in plants (Nazar et al. 2011; Osman and Rady 2012). Elemental sulfur, H_2S, GSH, PC, S-rich proteins, and various secondary metabolites are important S-containing defense compounds that are very important for plant survival during biotic and abiotic stresses. The development of these compounds in the plant is intimately linked to the supply, demand, uptake, and assimilation of S (Capaldi et al. 2015).

10.3 Sulfur Metabolism in Plants

Plants produce many S-containing metabolites of diverse groups: amino acids (Cys, Met), antioxidants (GSH), vitamins (biotin, thiamine), and secondary metabolites (glucosinolates, alliinase). Although these metabolites contain S, their roles in a biological system are functionally distinct. Thus, S metabolism in plants is a topic of interest to explain how S is assimilated into a living system from the environment (Fig. 10.2). Like other macronutrients, S is taken up by the plant through the root as sulfate (SO_4^{2-}). To be incorporated in the metabolic pathways, sulfate is first activated by ATP sulfurylase to yield adenosine-5′-phosphosulfate (APS) which is then reduced to sulfite (SO_3^{2-}) by APS reductase. Finally, sulfite reductase converts the sulfite into sulfide that reacts with O-acetylserine in the presence of O-acetylserine lyase (OAS-TL) to produce Cys (Fig. 10.2). From Cys, GSH is produced by two-step ATP-dependent reactions, where Cys is converted to γ-glutamylcysteine by γ-glutamylcysteine synthetase (also known as glutamate-cysteine ligase, GCL), and the subsequent reaction is catalyzed by glutathione synthetase. Cysteine also serves as a precursor of Met. Homocysteine is produced from cysteine and O-phosphohomoserine by the action of cystathionine γ-synthase (CGS) and cystathionine β-lyase (CBL) (Fig. 10.2). Homocysteine is then converted into Met by methionine synthase (MS). Methionine is considered as the main precursor of glucosinolate synthesis pathway by initiating the side chain elongation reaction to Met (Hirani et al. 2012). Cysteine conjugated with the tryptophan-derived complex is

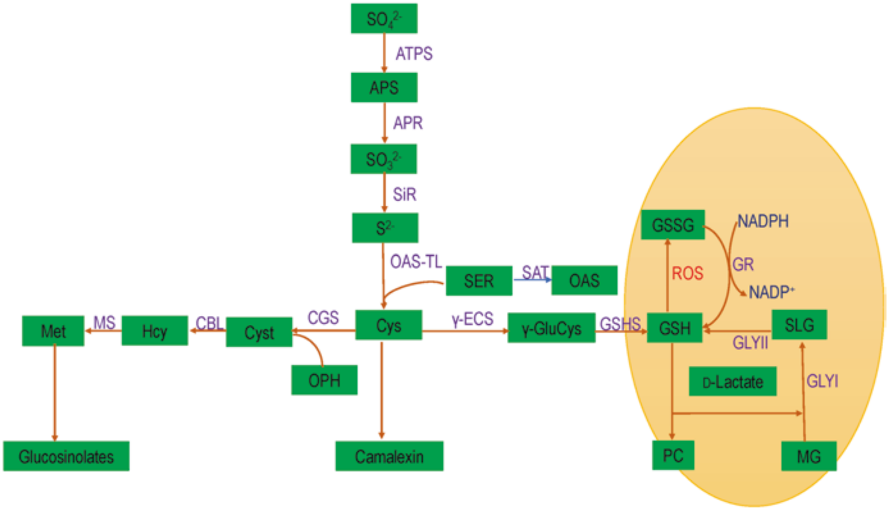

Fig. 10.2 Sulfate metabolism in plant. *APS*, adenosine-5′-phosphosulfate, *Cys* cysteine, *Cyst* cystathionine, *γ-GluCys* γ-glutamylcysteine, *GSH* glutathione, *GSSG* oxidized glutathione, *Hcy* homocysteine, *MG* methylglyoxal, *OAS* O-acetylserine, *OPH* O-phosphohomoserine, *PAPS* 3-phosphoadenosine-5-phosphosulfate, *SLG* S-D-lactoylglutathione, *Ser* serine, *APK* APS kinase, *APR* APS reductase, *ATPS* ATP sulfurylase, *CBL* cystathionine β-lyase, *CGS* cystathionine γ-synthase, *γ -ECS* γ-glutamylcysteine synthetase, *Gly I* glyoxalase I, *Gly II* glyoxalase II, *GR* glutathione reductase, *GSHS* glutathione synthetase, *MS* methionine synthase, *OAS-TL* OAS(thiol) lyase, *SAT* serine acetyltransferase, *SiR* sulfite reductase

involved in camalexin biosynthesis (Bottcher et al. 2009; Romero et al. 2014). Glutathione is a key regulator of redox signaling pathway and the antioxidant required for abiotic stress tolerance (Noctor et al. 2012). Glutathione is oxidized by reactive oxygen species (Noctor et al. 2012). The oxidized glutathione, GSSG, can be regenerated into GSH by GR. In addition, GSH is involved in two-step methylglyoxal (MG) detoxification: in the first step, MG is converted in S-D-lactoylglutathione (SLG) by glyoxalase I (Gly I) using GSH, and in the second step, D-lactate is produced from SLG by glyoxalase II (Gly II) releasing GSH (Hasanuzzaman et al. 2017b). The red circle marked in Fig. 10.2 is very responsive to different abiotic stresses.

Sulfur metabolism in the plant is greatly affected by environmental factors including biotic and abiotic factor. ATP sulfurylase activity or expression increases under sulfate starvation, salt stress, and light, Cd, and cold stress condition, and it contributes to abiotic stress tolerance (Khan et al. 2014; Anjum et al. 2015; Dixit et al. 2015b). Drought-induced alteration in S metabolic pathway in the plant is organ dependent. For example, drought stress decreased the Cys and GSH generation due to the lower assimilation of S in maize leaf. However, Cys, total glutathione, and SO_4^{2-} content were higher in the root (Ahmad et al. 2016). Salinity induced threefold higher expression of APS reductase (APR) in *Arabidopsis* roots (Koprivova and Kopriva 2008). However, salt stress induced by Na_2SO_4 decreases the expression of APR in roots of *Brassica rapa* but not affected by NaCl, indicating APR expression depends on sulfate availability (Reich et al. 2017). Cadmium stress (10 mg kg^{-1}) enhanced the activity of enzymes (ATPS, OASTAL, γ-ECS) of S assimilatory pathway in both root and shoot of *Brassica chinensis* L. (Lou et al. 2017). Above mentioned reports suggest that environmental stresses can alter the metabolic pathway of S. Therefore, this pathway could be the potential target for enhancing abiotic stress tolerance since there are few reports on this topic.

10.4 Sulfur Transporters in S Metabolism

As an inorganic molecule, S first needs to get into the cell. There are many membrane-bound transport proteins that facilitate the entry of nutrient inside the root from the outer environment. A motive force generated due to proton gradient mediates the sulfate influx using H^+/SO_4^{2-} cotransport system. To be metabolized into different metabolites, both inorganic forms of S and an organic molecule containing S must pass the membrane of cellular compartments through transport proteins. Smith et al. (1995) isolated three cDNAs from *Stylosanthes hamata* encoding sulfate transporters, which were highly conserved in other biological organisms: fungi, yeast, plants, and mammals. The two high-affinity H^+/SO_4^{2-} cotransporters, *shst1* and *shst2*, facilitate sulfate uptake from sulfur-deficient media, whereas the low-affinity H^+/SO_4^{2-} cotransporter, *shst3*, transports sulfate to the cellular compartments. All the above mentioned sulfate transporters (SULTRs) contain characteristic 12 putative membrane-spanning domains and STAS (sulfate transporter and anti-sigma factor antagonist) domain playing a role in protein folding and regulating protein activity, respectively (Takahashi 2010; Takahashi et al. 2011). With time some sulfate transporter has been reported in *Brassica oleracea*, potato, and tomato (Buchner et al. 2004; Hopkins et al. 2005; Howarth et al. 2003). Also, 12 sulfate transporters gene were identified in *Arabidopsis* using modern genomic tools and techniques. These transporter proteins are classified into four groups, which have distinct functions; group 1 includes high-affinity SULTRs, while group 2 consists of low-affinity transporters. Both group 1 and group 2 SULTRs mediate SO_4^{2-} uptake from nutrient media. Unlike groups 1 and 2, group 3 includes the transporter localized in plastid and symbiosome membrane playing specific function, sometimes unknown function, whereas group 4 mediates the SO_4^{2-} transport from the vacuole to other cell organelles (Takahashi 2010; Gigolashvili and Kopriva 2014). Localization and expression of sulfate transporters indicate their function in the sulfate metabolism (Table 10.1).

High-affinity sulfate transporters (SULTR1;1, SULTR1;2) categorized in group 1 play a role in the initial uptake of sulfate from the growing media (Takahashi 2010; Takahashi et al. 2011). Yeast mutant lacking *Sultr1;1* showed lower sulfate uptake, while mutant containing overexpressed *Sultr1;1* vector improved sulfate uptake confirming SULTR1;1 is a sulfate transporter (Takahashi et al. 2000). Based on phylogenetic tree relationship and sequence information, it was predicted that other sulfate transporters might be present in the root having similarity in functions

Table 10.1 Sulfate transporters in plants and their function and localization in cell

Group	Transporter gene	Expression organs and tissue localization	Functions	References
1	SULTR1;1	Localized in root hairs, epidermis and cortex, expressed in cell layers	Initial uptake of sulfate from nutrient media	Takahashi et al. (2000)
	SULTR1;2	Localized in root hairs, epidermis and cortex, expressed in cell layers	Initial uptake of sulfate from nutrient media	Shibagaki et al. (2002)
	SULTR1;3	Localized in companion cell of phloem, expressed in both shoot and root	Transport of sulfur from source to sink and uptake of sulfur in phloem companion cell when other transporters are repressed	Yoshimoto et al. (2003) and Takahashi et al. (2000)
2	SULTR2;1	Expressed in root pericycle and xylem parenchyma, as well as in xylem and phloem parenchyma of shoots	Facilitate distribution of sulfate to leaf tissue	Takahashi et al. (2000)
	SULTR2;2	Expressed in companion cell of phloem	Transport of sulfate through root phloem and transfer it to the site of sulfur assimilation	Takahashi et al. (2000)
3	SULTR3;1	Localized in chloroplast, expressed in leaves	Facilitate sulfate uptake in the chloroplast	Cao et al. (2013)
	SULTR3;2	Expressed in leaf	Facilitate sulfate uptake in the chloroplast	Cao et al. (2013)
	SULTR3;3	Expressed in leaf	Facilitate sulfate uptake in the chloroplast	Cao et al. (2013)
	SULTR3;4	–	Facilitate sulfate uptake in the chloroplast	Cao et al. (2013)
	SULTR3;5	Colocalized in root, expressed in root pericycle and xylem parenchyma	Play a role in root to shoot transport	Kataoka et al. (2004b)
4	SULTR4;1	Localized in tonoplast, expressed in root and shoot	Remobilize sulfate from vacuole and regulate transport of sulfate from root to shoot	Kataoka et al. (2004a)
	SULTR4;2	Localized in tonoplast, expressed in root and shoot	Remobilize sulfate from vacuole and regulate transport of sulfate from root to shoot	Kataoka et al. (2004a)

and affinity to sulfate (Takahashi et al. 2000). Selenate-resistant mutant showed lower uptake of sulfate both in sulfur-sufficient and sulfur-deficient medium. By yeast complementation technique, it is proved that the mutant was lacking *Sultr1;2* gene, which is responsible for sulfate uptake in the root (Shibagaki et al. 2002). Interestingly, either SULTR1;1 or SULTR1;2 is not involved in root to shoot transport which indicates the involvement of other sulfate transporters to facilitate sulfate transport from the root to shoot. Getting entry through root hairs, sulfate reaches the endodermis to epidermis and cortex followed by xylem parenchyma through the symplastic pathway. However, sulfate can get entry to xylem parenchyma from the apoplast by SULTR2;1 (Maruyama-Nakashita et al. 2003). Mutant in *Sultr3;5* restricted the transport of sulfate root to shoot. However, *Sultr2;1* coexpressed with *Sultr3;5* increased the root to shoot transport compared to *Sultr2;1* expressed alone (Kataoka et al. 2004b; Takahashi et al. 2011). Furthermore, *Sultr2;1* is found to be expressed in the leaf phloem suggesting its role in the reduction of excess sulfate from above ground part (Takahashi et al. 2000). SULTR2;2 transports sulfate to the mesophyll and palisade cell of leaf unloading from the xylem vessel (Takahashi et al. 2000). Under sulfate-deprived condition, overexpressed *Sultr1;3* facilitates sulfate uptake in the phloem companion cell as *Sultr2;1* repressed under sulfate-deficient condition (Yoshimoto et al. 2003; Takahashi 2010). When excess in supply, sulfate is reserved in the vacuole, but sulfate influx mechanism into the vacuole has not been well studied. However, the efflux of sulfate from the vacuole into the cytoplasm is mediated by SULTR4;1 and SULTR4;2 transporter protein, categorized in group 4 (Kataoka et al. 2004a). With these transporters, sulfur is taken up by roots and subsequently transported to different organs. Finally, sulfate gets into chloroplast where sulfur assimilatory pathway takes place. Using green fluorescent protein (GFP), SULTR3;1 transporter localization in the chloroplast was confirmed. Furthermore, mutant that lack this transporter showed lower sulfate uptake in the chloroplast, indicating SULTR3;1 is associated with sulfate transport in the chloroplast (Cao et al. 2013). Like SULTR3;1, other sulfate transporters like SULTR3;2, SULTR3;3, and SULTR3;4 are also involved in sulfate transport in the chloroplast (Cao et al. 2013). Among the four groups of sulfate transporters, transporters categorized in group 3 are less investigated compared to the others. For example, SULTR3;2-, SULTR3;3-, and SULTR3;4-mediated sulfate uptake mechanisms are still not clear.

10.5 Sulfate Transporter and Abiotic Stress

Different environmental factors including soil salinity, drought, waterlogging, high temperature, chilling, and heavy metal (HM) stresses affect nutrient metabolism from transport to assimilation. Under such extreme conditions, transporter proteins fail to function properly. As a result, ion homeostasis or nutrient balance is disrupted. Glutathione, a sulfur derivative compound, plays a diverse role under abiotic stress condition. In the presence of selenium (Se), reduction in endogenous GSH has a regulatory role in the expression of primary sulfate uptake transporter *Sultr1;1* (Takahashi et al. 2000; Fig. 10.3). Abscisic acid is a key factor to regulate abiotic stress tolerance. Surprisingly, a mutant lacking sulfate transporter *Sultr3;1* showed lower abscisic acid (ABA) content both in control and salt stress (200 mM NaCl) condition compared to wild type (Cao et al. 2014). This result indicates the

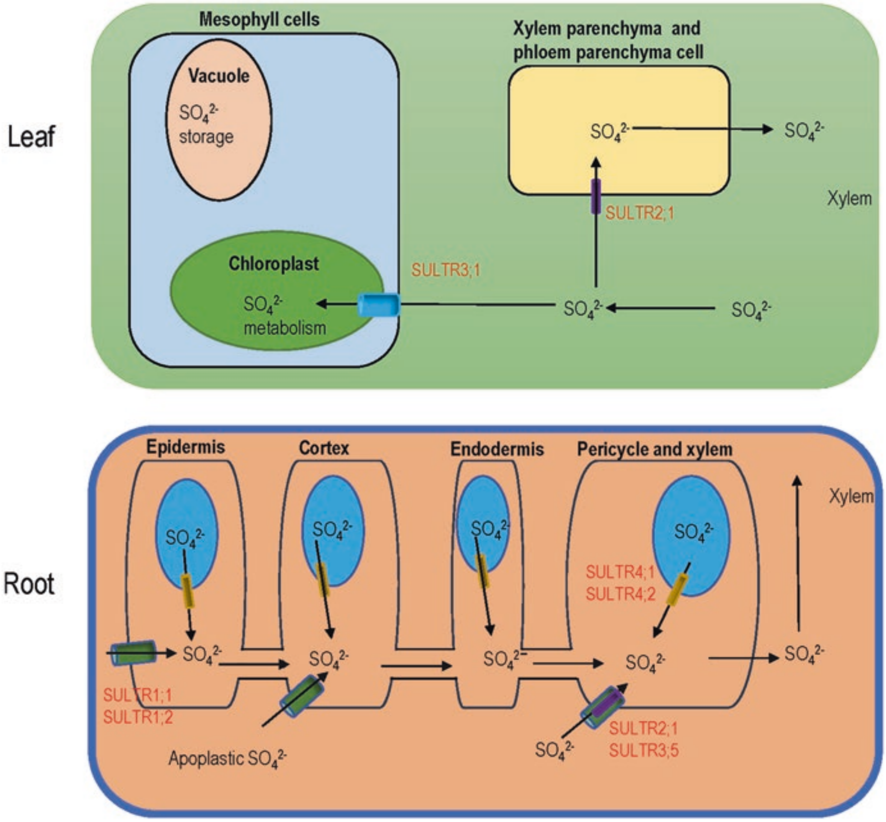

Fig. 10.3 Role of sulfate transporters in sulfate uptake and distribution (Adapted from Takahashi et al. (2011))

possibility of sulfate transporters to be involved in abiotic stress tolerance. In *Medicago truncatula*, almost all sulfate transporters are affected by either drought or salinity (Gallardo et al. 2014). Under HM stresses in particular Cd stress, sulfate uptake increases due to the expression of *ZmST1;1*, very similar to high-affinity sulfate transporter which belongs to group 1 (Table 10.1). Higher sulfate uptake is associated with higher production of PC to detoxify toxic Cd (Nocito et al. 2006). Another high-affinity sulfate transporter *Sultr1;2* is proved to be associated with As stress tolerance as *Arabidopsis* mutant lacking *Sultr1;2* showed sensitivity to As in response to growth parameters (Nishida et al. 2016). The expression of sulfate transporters may vary from the shoot to root under unfavorable condition. For example, under prolonged drought for 10 and 12 days, *Sultr1;2* expression reduced in the leaf and not affected in the root. However, *Sultr4;1* overexpressed in leaf but repressed in roots. This result suggests that with the help of this transporter maize seedling maintained S homeostasis in the root. As a result root growth increased in search of water (Ahmad et al. 2016). As SULTRs are distinguishable in function, their responses also vary depending on the type of stresses, indicating a particular transporter may play a role in tolerance of a particular type of stress. Though there are many indirect pieces of evidence that explain the involvement of sulfate transporter in abiotic stress tolerance, still this hypothesis needs further confirmation with rigorous experimental evidence.

10.6 Exogenous Use of Sulfur in Improving Plant Performances Under Abiotic Stress

Environmental stressors affect cell homeostasis inside plant tissue, and increasing ROS production leads to oxidative damage (Boaretto et al. 2014; Hasanuzzaman et al. 2017). Sulfur is an indispensable macronutrient for plant growth, development, and survival, and at the same time, many S-containing compounds play defensive roles in abiotic stress response, as well as cellular acclimation and adaptation in adverse condition (Cao et al. 2014). Plants respond to abiotic stresses in many ways, but the S assimilation pathway, the important source of reduced S for a variety of cellular mechanisms including Cys synthesis, which further used for Met biosynthesis or GSH production (Siddiqui et al. 2012). Thus the exogenous supply of S helps plants to survive in stress condition by maintaining their usual metabolic process (Table 10.2).

It seems that the HM/metalloid stress increases the demand of reduced S, hence activating the expression of SO_4^{2-} transporters and enzymes in the S assimilatory pathway (Takahashi et al. 2011; Hawkesford 2012). Therefore, many research reports have shown the effect of exogenous S in mitigating various abiotic stresses. Sulfur has a vital role in nutrient homeostasis; thus, it can decrease the uptake of the HMs/metalloids and at the same time increase the absorption of essential plant nutrients. On the other hand, exogenous S may increase the uptake of few HMs/metalloids, thus may be further useful for phytoremediation. In As-stressed plants increased S supply increases thiol metabolism and antioxidant activity, As accumulation, as well as tolerance of plants (Srivastava and D'Souza 2010). Sulfate nutrition plays an important role in regulating As translocation from roots to shoots, possibly through the complexation of AsIII-PCs in rice (Zhang et al. 2011). Conclusively S supplementation reduced the As accumulation in a shoot by increasing thiol metabolism and glycolysis toward amino acid accumulation under AsIII stress in rice (Dixit et al. 2015a). Sheng et al. (2016) found a moderate level of S application, beneficial to wheat against Mn toxicity, via upregulating the antioxidant defense, and the translocation and distribution of Mn from roots to shoots, excess Mn sequestering in vacuoles in the form of PCs, and increased production of GSH, where GSH played a very important role. Applying S in guinea grass may be a vital tool for phytoremediation of Cu under Cu toxicity in Cu-polluted areas, by increasing Cu uptake as well as increasing (30–40% higher) shoot and root dry mass and decreasing of lipid peroxidation (Gilabel et al. 2014).

Table 10.2 Studies showing beneficial response of exogenous sulfur and its derivatives in plants conferring various abiotic stresses

Plant species	S treatment	Abiotic stressors	Protective effects	References
Brassica napus var. Xiangnongyou 5710	Elemental S, 60 kg ha^{-1}	Se (Se 60 g ha^{-1} applied as $Na_2SeO_4.10H_2O$)	Reduced Se and erucic acid content in seed	Liu et al. (2017)
			Increased seed yield and seed oil content	
Hydrilla verticillata	2.0 mM as $MgSO_4$	As (50 mM Na_2HAsO_4)	Increased total thiols and antioxidant content, except CAT	Srivastava and D'Souza (2010)
			Improved redox status	
Oryza sativa cv. IR-36	5.0 mM S as SO_4^{2-}	As ($NaAsO_2$ 25 µM and (Na_2HAsO_4 50 µM)	Increased root As accumulation and restricted As translocation to the shoots	Dixit et al. (2015b)
			Enhanced synthesis of NPTs and PCs	
			Counterbalanced redox state and reduce H_2O_2 content	
			Improved activity of APR, CS, SAT, γ-ECS, GR and SOD, APX, GPX, CAT, AR, and AO except γ-glutamyl transpeptidase (γ-GT), GST	
O. sativa cv Jiahua 1	0.7 mM SO_4^{2-}	As (10 µM arsenite/10 µM arsenate)	Reduced As in root and translocation to shoot	Zhang et al. (2011)
			Increased NPT and PCs and GSH content	
O. sativa cv IR-36	5.0 mM SO_4^{2-}	As (25 µM $NaAsO_2$)	Reduced As accumulation in shoot	Dixit et al. (2015a)
			Improved glycolysis, thiol metabolism, and antioxidant enzyme activity	
B. juncea cv. Pusa Jai Kisan (ethylene-sensitive) and SS2 (ethylene-insensitive)	1.0 mM SO_4^{-2} as $MgSO_4$	Cd (0.50 mM Cd as $CdCl_2$)	Reduced thiobarbituric acid reactive substances (TBARS) and H_2O_2 and ethylene content	Asgher et al. (2014)
			Upregulated SOD, APX, GR, SAT, ATPS, ACS, and RuBisCO activity	
			Increased Cys and GSH content	
			Promoted photosynthesis and dry mass accumulation	

(continued)

Table 10.2 (continued)

Plant species	S treatment	Abiotic stressors	Protective effects	References
B. chinensis cv. Aikangqing and Qibaoqing	4 mM Na_2SO_4	Cd (0.1 mM $CdCl_2$)	Decreased Cd content, MDA, and $O^{2\bullet-}$ in both root and shoot; increased NPT, PCs, GSH, AsA, and redox state in both root and shoot	Liang et al. (2016)
B. chinensis cv. Aikangqing and Qibaoqing	50 mg Na_2SO_4 kg^{-1} soil	Cd (1 mg and 10 mg $CdCl_2.5H_2O$ kg^{-1} soil)	Increased growth	Lou et al. (2017)
			Stimulated antioxidant enzymes	
			Upregulated ASA-GSH cycle and S assimilation	
			Boosted PC and NPT production	
B. juncea cv. Pusa Jaikisan	300mMSO_4^{2-}	Cd (100 mM $CdCl_2$)	Reduced TBARS content while increased AsA and GSH, PCs, NPT, and chl contents and balanced redox state	Bashir et al. (2015)
			Upregulated SOD, CAT, APX, and GR activity	
Triticum aestivum cv. Yan Long 19	1.5 mM Na_2SO_3/ $NaHSO_3$ (3:1)	Cd (1.0 mM $CdCl_2$)	Increased H_2S content; amylase and esterase activity thus elevated reducing sugars and soluble protein levels in germinating seeds	Hu et al. (2014)
			Reduced MDA, H_2O_2, and $O_2^{\bullet-}$ generation and retained plasma membrane integrity of the radical tips	
			Boosted the activity of POX, APX, SOD, and CAT and reduced LOX activity	
T. polonicum	10mMSasSO_4^{2-}	Mn (3.0 mM Mn)	Improved GSH production and sequestering surplus Mn in vacuoles	Sheng et al. (2016)
			Inhibited translocation of Mn from roots to shoots	
			Stimulated antioxidant enzymes	

(continued)

Table 10.2 (continued)

Plant species	S treatment	Abiotic stressors	Protective effects	References
Panicum maximum cv. Tanzânia	2mMSasSO_4^{2-}	Cu (1000 μM Cu)	Increased Cu uptake and translocation Osmotic adjustment via Pro Nonsignificant but reduced MDA and H_2O_2 content	Gilabel et al. (2014)
T. aestivum	1.2 mM SO_2 as $NaHSO_3$/Na_2SO_3	Al	Reduced the accumulation of $O_2^{\bullet -}$, H_2O_2, and MDA Enhanced the activities of POX, CAT, and APX and decreased the LOX activity	Zhu et al. (2015)
Arabidopsis thaliana (ecotype Columbia, Col-0)	1500 μM S as SO_4^{2-}	Salinity (200 mM NaCl)	Upregulated some antioxidant enzyme and kept steady-state ABA level	Cao et al. (2014)
B. juncea var. Varuna	Elemental S 200 mg kg^{-1} soil	Salinity (100 mM NaCl)	Reduced Na^+ and Cl^- content of leaf Increased ATP-S activity, RuBisCo activity, Cys content, GSH content, and redox state Amplified chl content, stomatal conductance, PSII activity, and net photosynthesis Increased leaf area and dry mass	Fatma et al. (2014)
Fragaria × *ananassa* cv. Camarosa	100 μM NaHS	Salinity (100 mM NaCl) and drought (10% PEG 6000)	Increased leaf chl fluorescence, stomatal conductance and leaf relative water content, and NO levels Lowered MDA and H_2O_2 levels and balanced redox state	Christou et al. (2013)
Capsicum annum	S (5 and 10 g L^{-1} of nutrient solution)	Salinity (5 dS m^{-1} EC using NaCl)	Enhanced growth, leaf number, fruit number and weight, photosynthesis rate, and stomatal conductance Reduced Na^+ content in leaf and increased Pro and glycine betaine (GB) production in both root and shoot	Mukhtar et al. (2016)

(continued)

Table 10.2 (continued)

Plant species	S treatment	Abiotic stressors	Protective effects	References
A. thaliana (ecotype Columbia-0)	100 mM NaHS	Salinity (150 mM NaCl)	Increased seedling survival rate	Shi et al. (2015)
			Decreased generation of $O_2^{\bullet -}$ and	
			H_2O_2 and balanced GSH redox state	
			Upregulated SOD, CAT, POD, and GR activity	
A. thaliana (ecotype Columbia-0)	S as 100 mM NaHS	Drought	Increased seedling survival rate	Shi et al. (2015)
			Decreased generation of $O_2^{\bullet -}$ and	
			H_2O_2 and balanced GSH redox state	
			Upregulated SOD, CAT, POD, and GR activity	
B. juncea cv. Red Giant	Elemental S as 3 mM $CaSO_4$	Drought (50% of well-watered)	Increased levels of aliphatic glucosinolates in leaves and roots followed by decrease in ABA content	Tong et al. (2014)
T. aestivum cv. Luyuan 502 and Jimai 22	0.15 mM NaHS	Heat stress (38/28 °C day/night temperature, respectively)	Increased activities of SOD, CAT (decreased in Jimai 22), and APX; higher H_2S and soluble sugar contents but lower H_2O_2 and MDA contents	Min et al. (2016)
Nicotiana tabacum	50 µM NaHS	Heat stress (43 °C)	Increased sulfhydryl compounds (H_2S, Cys, GSH), upregulated antioxidant enzymes SOD, CAT, POX, and GR	Li et al. (2015)
A. thaliana (ecotype Columbia-0)	100 mM NaHS	Freezing (4 °C)	Increased seedling survival rate	Shi et al. (2015)
			Decreased generation of $O_2^{\bullet -}$ and H_2O_2 and balanced GSH redox state	
			Upregulated SOD, CAT, POD, and GR activity	

Application of S to Cd-stressed pak choi (*Brassica chinensis* L.) plants enhanced Cd tolerance by promoting the AsA-GSH cycle and PC biosynthesis. After application of S exogenously, its assimilation increased by the activity of ATP sulfurylase (ATPS) and O-acetylserine (thiol) lyase (OAS-TL) and decreased Cd translocation from the roots to the shoots (Liang et al. 2016; Lou et al. 2017). Indian mustard (*Brassica juncea*) plant supplemented with S under Cd stress accumulated the higher amount of AsA and GSH content as well as improved AsA/DHA, and GSH/GSSG ratio indicated the role of exogenous S in producing GSH, NPTs and PCs, and tolerance against Cd stress (Bashir et al. 2015). A similar result was also found by other researchers in *B. juncea* which suggested that Cd stress overproduced ethylene, which can be alleviated with S by antioxidant (GSH) metabolism (Asgher et al. 2014). Under Cd stress, seed priming with the SO_2 donor moderately increased the amylase and esterase activities and increased the levels of reducing sugars and soluble protein in germinating wheat seeds. Pretreatment with the SO_2 donor also reduced the MDA and and $O_2^{\bullet-}$ and restrain the plasma membrane integrity of the wheat seedlings radical tips as well as increase the activity of POD, APX, SOD, and CAT while reducing the activity of LOX (Hu et al. 2014). Zhu et al. (2015) reported a higher level of H_2S in wheat seeds primed with the SO_2 donor ($NaHSO_3/Na_2SO_3$). Wheat seed pretreated with 1.2 mM $NaHSO_3/Na_2SO_3$ reduced overaccumulation of $O_2^{\bullet-}$, H_2O_2, and MDA, with lower lipoxygenase (LOX) activity, while the activity of guaiacol peroxidase (POD), CAT, and APX increased to enhance tolerance against Al toxicity (Zhu et al. 2015).

Tobacco cell culture pretreated with the H_2S donor, sodium hydrosulfide (NaHS), $KHSO_3$, and precursor Cys significantly increased the survival percentage of tobacco cells under high heat (Li et al. 2015). They also found an elevated level of sulfhydryl compounds such as H_2S, sulfhydryl proteins, Cys, and GSH as well as higher antioxidant enzyme activity, for instance, SOD, CAT, cell wall peroxidases (POX), and GR, by pretreating with NaHS. Meanwhile, NaHS-pretreated wheat seedlings were found with higher antioxidant defense and H_2S and soluble sugar contents, while lesser H_2O_2 and MDA contents are induced by heat stress. But the little effect was found regarding antioxidant enzyme activities and other soluble substance levels compared to control (Min et al. 2016). In cluster beans under heat stress, S supplementation helps to mitigate the oxidative stress with higher AsA-GSH content and to lower the H_2O_2, MDA, and electrolyte leakage. Sulfur also increased dry weight and chl content under heat stress (Mobin et al. 2016). The study explored that pretreatment of strawberry roots with NaHS (100 μM for 48 h) could induce long-lasting tolerance to salinity (100 mM NaCl) or drought (10% PEG-6000) for 7 days. Furthermore, NaHS pretreatment resulted in lower NO and H_2O_2 content in leaves along with high AsA and GSH content, following salt and drought stresses. Thus, H_2S pretreatment managed the plants to overcome the salt and drought stress through upregulating antioxidant defense mechanisms and the coordination of the salt overly sensitive (SOS) pathway in strawberry (Christou et al. 2013). Salt stress drastically reduces the yield of crops by ionic toxicity and physiological drought. But exogenous S application from a foliar spray can mitigate the salinity stress by increasing photosynthetic rate, stomatal conductance, chl content, Pro, and GB content. The result suggested that S at both 5 and 10 g L^{-1} of spray solution improved the morphophysiological and biochemical traits in chili plants subjected to salinity (Mukhter et al. 2016). While working with mustard, Fatma et al. (2014) reported that excess S in the soil more rapidly alleviated the negative effects of salinity and improved photosynthesis and growth by increased GSH production. To support their statement, they again applied 1 mM GSH exogenously and found similar results of that excess S supplementation and confirmed excess S/GSH as a potential protectant against salt stress. At the time of salt stress, Cys is required to produce ABA to combat stress, while S supplementation increased the Cys production for ABA biosynthesis (Cao et al. 2014).

10.7 Sulfur Derivatives and Their Roles in Abiotic Stress Tolerance

Overproduction of ROS and MG is an inevitable process that occurs in different tissue types, under a diverse adverse environmental conditions including salinity, drought, toxic metal, high temperature, low temperature, waterlogging, etc., which might be regulated by a number of defensive molecules or systems in plants (Hasanuzzaman et al. 2012, 2017a; Sharma et al. 2012). Sulfur-containing compounds, for example, GSH, H_2S, Met, Cys, PC, ATP-S, protein thiols, etc., play an immense role in normal functioning of the plant cell (Fig. 10.4). Also, such S derivatives primarily work in plant stress tolerance (Colville and Kranner 2010; Zagorchev et al. 2013). Under stress condition in most of the cases, the content of endogenous S-containing compounds increased up to a certain extent to protect plants from respective stress (Khan et al. 2013; Zagorchev et al. 2013; Hasanuzzaman et al. 2017b). Recently the exogenous application of different S derivatives (GSH, H_2S, etc.) against a variety of abiotic stresses is receiving attention due to their effectiveness in enhancing stress tolerance.

Sulfur-rich Cys is very important for plants not only as an amino acid but also due to its role as a precursor for a huge number of vital biomolecules (Haag et al. 2012). Cysteine possesses a vital position in plant metabolism because it plays an essential role in the biosynthesis of important S-containing cellular compounds, for example, GSH and different proteins (Romero et al. 2014). These compounds directly or indirectly work in the redox signaling pathway and stress tolerance mechanisms. Moreover, Cys triggers metabolism of nitrogen at the biochemical and molecular level which plays an imperative role in enhancing plant stress tolerance (Zagorchev et al. 2013; Erdala and Turk 2016). On the other hand, Cys is a powerful metal chelator, but Cys-metal ion complexes are capable of activating the most devastating Fenton reaction, which may create toxic $OH^{\bullet}$ radical in a plant cell (Bashir et al. 2012). Though endogenous Cys played a great function in a plant cell, the exogenous application of Cys for alleviating abiotic stress from the plant is very rare. Erdala and Turk (2016) demonstrated that Cys application to maize seedlings

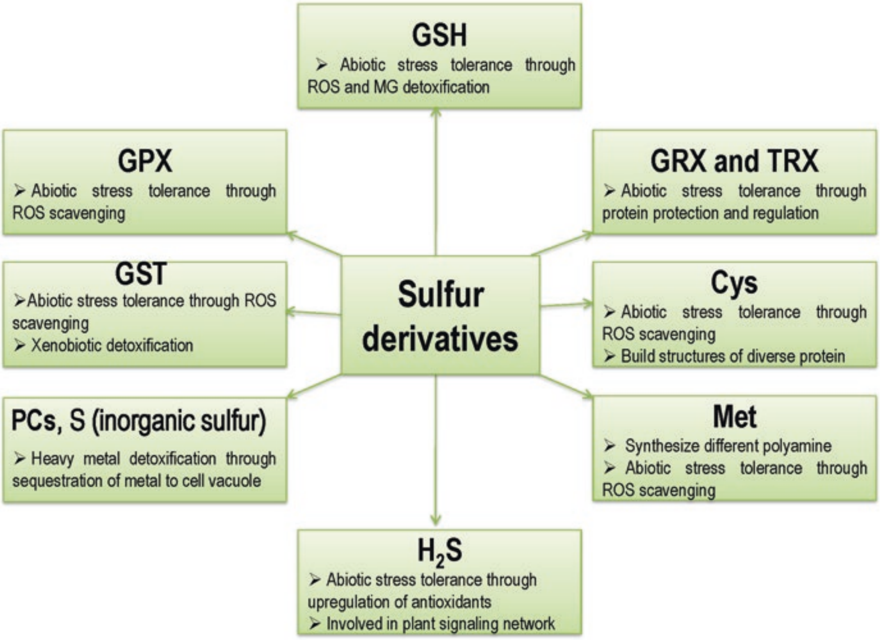

Fig. 10.4 Roles of S derivatives in abiotic stress tolerance of plant

mitigates Cd-induced oxidative stress. Like Cys, Met can undergo ROS-mediated oxidation through a class of cytosolic and plastidic enzymes that are involved in mitigating the oxidative damage of plant (Dos Santos et al. 2005; Cabreiro et al. 2006). Methionine is also a substrate for the synthesis of a range of polyamines (putrescine, spermidine, spermine, etc.), which has important roles in stress tolerance (Alcázar et al. 2010).

Sulfate is first activated by ATP-S to yield APS which is then reduced to SO_3^{2-} by APS reductase and then further reduced to S^{2-} and finally incorporated into Cys which helps to produce S-rich GSH. So, enhancement of ATP-S in a plant cell is very urgent for developing plant stress tolerance. Glutathione is one of the most important nonenzymatic antioxidants for living systems which plays a noteworthy role in cellular metabolism and works as a vital component in scavenging of toxic ROS in a plant cell (Gill and Tuteja 2010; Hasanuzzaman et al. 2012; Noctor et al. 2012; Nahar et al. 2016). Also, it works in glyoxalase system to detoxify toxic MG (Hasanuzzaman et al. 2017a). By upholding the reduced status of α-tocopherol and zeaxanthin, GSH protects the membrane of the cell, which contributes to the reduction of protein denaturation under stress condition. Moreover, it functions as a substrate of glutathione peroxidase (GPX) and glutathione *S*-transferase (GST). Both GPX and GST play a direct role in scavenging of toxic ROS and protecting plants from oxidative stress induced by different abiotic stresses (Hasanuzzaman et al. 2012; Asgher et al. 2017). Glutathione *S*-transferase is also involved in detoxification of xenobiotics (Zagorchev et al. 2013). Glutathione, as a precursor of PC, assists in metal chelation, which transfers the toxic metals or metalloids to the cell vacuole as an inactive form (Hasanuzzaman et al. 2017a, b; Sharma and Dietz 2006). Consequently, it acts an imperative function in detoxification of toxic metals/metalloids (Hasanuzzaman et al. 2017b; Srivalli and Khanna-Chopra 2008). In addition to a variety of functions of GSH reported before, there is a confirmation that GSH is highly associated with controlling different genes (Zagorchev et al. 2013). Such abovementioned biochemical characteristics of GSH make it indispensable for plant growth and development under both usual and adverse growing conditions. Many previous reports confirmed that endogenous or exogenous GSH contributes to increase tolerance level of plants to diverse abiotic stresses, including salinity, drought, high temperature (HT), low temperature, and toxic metal stress (Kumar et al. 2010; Mahmood et al. 2010; Wang et al. 2011; Wu et al. 2011; Chen et al. 2012; Hasanuzzaman et al. 2012; Jozefczak et al. 2012). Here, we discussed few recent findings. Cheng et al. (2015) reported that exogenous application of reduced GSH in *Arabidopsis* plant could improve abiotic stress tolerance. They also claimed that endogenously enhanced GSH bestowed tolerance on the same plant under salt and drought stress. Furthermore, senescence and flowering are delayed due to both exogenous and endogenous GSH. Their translatome analysis also uncovered that GSH treatment triggered the biosynthesis process of ABA, auxin and jasmonic acid (JA), as well as signaling genes, which might be helpful for increasing plant stress tolerance. Çevik and Ünyayar (2015) checked the function of exogenously applied AsA and GSH on antioxidant system of *Cicer arietinum* plant under drought stress and observed that both GSH and AsA contribute to enhancing tolerance level against drought stress in chickpea. Nahar et al. (2015a) reported that exogenous GSH enhances the activity of most of the enzymes of antioxidant defense system (APX, MDHAR, DHAR, GR, GPX, GST, SOD and CAT) and glyoxalase system of drought-affected mung bean plant either considerably or slightly. Accordingly, GSH reduced the content of over-generated ROS and MG which finally successfully decreased the oxidative damage. But the performance of GSH was day dependent. With the increasing stress duration, GSH showed lower effectivity to counter stress. A similar trend of positive findings was recorded due to exogenous GSH in the same plant under high temperature (HT) and salt stress (Nahar et al. 2015b, c). Compared to only stress supplementation of GSH in HT-stressed cucumber plants, considerably increased soluble protein content, proline level, activities of different antioxidants and their associated gene expression, as well as exogenous GSH reduced the ROS production and decreased the cell lipid peroxidation (Ding et al. 2016). Their results suggest that exogenously applied GSH improve tolerance level of HT-stressed cucumber plants due to its positive action in water status, photosynthetic process, and antioxidant defense system. Khan et al. (2016) demonstrated that exogenous GSH application decreased MDA and H_2O_2 content of cotton leaves because of increased activity of POD, APX, GR, SOD, and CAT. These findings recommended that exogenous application of GSH decreased the undesirable effects of Pb and enhanced tolerance of cotton plants to oxidative stress. Glutathione enhanced the manufacture of NO and total S-nitrosothiol contents and upheld a reduced cellular redox status and increased antioxidant capacity along with induction of transcripts of transcription factors and antioxidant genes under Cd stress in tomato plants (Hashem et al. 2016). Similarly, Daud et al. (2016) observed the GSH-mediated oxidative stress tolerance in the cotton plant under Cd stress. Therefore, it is very obvious that any source of GSH either endogenous or exogenous develop plant stress tolerance under the adverse growing condition, but success depends on the interaction of it to the stress regarding the proper amount of GSH.

Even though H_2S is considered as a phytotoxin, it is documented that plants can themselves produce and liberate this gas, particularly when uncovered to external Cys, sulfate, sulfite, or SO_2 (Li 2013; Li et al. 2016; Wei et al. 2017). Maybe for the indulgence of excess S, the plant goes through such mechanism. Nevertheless, under few biotic and abiotic stresses, plants release H_2S more than basal, endogenously produced rates (Jin et al. 2011; Wei et al. 2017). Additionally, as a vital sulfur compound, H_2S works in various developmental processes of plant and contributes to enhance plant stress tolerance as it can upregulate the transcripts of multiple abiotic and biotic stress-related genes and hinder accumulation of ROS (Shi et al. 2014; Li and Hey 2015; Chen et al. 2017). Endogenous H_2S accumulation is a widespread feedback of plants to environmental stress, including salt, drought, HM/metalloid, and heat and cold stress which might be intimately connected with the acquisition of plant stress tolerance (Li 2013; Calderwood and Kopriva 2014; Hancock and Whiteman 2014). Hydrogen sulfide is involved in a complex signaling network consisting of many secondary messengers such as Ca^{2+}, ABA, H_2O_2, and NO, which protect the plant from stress-induced damage (Li et al. 2016). In recent time, low concentration of exogenous H_2S is emerging as a novel gaseous signal molecule which confirmed its positive effect in different plants under normal and adverse growing condition. It has numerous positive functions on plant growth and development. The action of supplemented H_2S is also found to enhance plant stress tolerance under environmental difficulties (Li 2013; Li et al. 2016). Interestingly, exogenous application of H_2S confirms considerable positive effects on germination of seed (Li and He 2015; Wojtyla et al. 2016), plant growth and development (Fang et al. 2014), and regulation of senescence (Zhang et al. 2011), with the increasing of plant stress tolerance against salt (Christou et al. 2013; Chen et al. 2015; Deng et al. 2016), drought (Christou et al. 2013; Shen et al. 2013; Chen et al. 2016; Ma et al. 2016), toxic metal (Chen et al. 2013, 2017; Cui et al. 2014), high temperature (Li et al. 2013a,b; Li 2015), and cold stress (Fu et al. 2013; Du et al. 2017). The above functions of H_2S signify that it might be a promising candidate for signal transduction in plant's cross-adaptation. Recently, Chen et al. (2017) observed that H_2S acted as an antioxidant and scavenged ROS through regulating different antioxidant enzymes, thus preventing metal-induced (Hg) oxidative damages. In contrast to stressed plant, exogenous application of H_2S in drought-affected wheat seedlings increased the activity of different antioxidant enzymes and reduced ROS production and lipid peroxidation in both leaves and roots. Moreover, H_2S addition in plants enhanced ABA biosynthesis, which participated in developing drought stress tolerance (Ma et al. 2016). In parallel, Chen et al. (2016) found that H_2S regulates the polyamines and sugar changes in *Spinacia oleracea* seedlings under drought stress condition, which provided stress tolerance for the plants. Exogenously applied H_2S in salt-affected plants maintained the balance between Na^+ and K^+ in growing media and cell along with upregulation of different ROS scavenging enzymes, which maintained the cellular balance and protected plant from the salt-induced damages (Christou et al. 2013; Chen et al. 2015; Deng et al. 2016). A similar type of actions of H_2S in enhancing stress tolerance was observed under other abiotic stresses including heat and cold stress (Li et al. 2013a, b; Fu et al. 2013; Li 2015; Du et al. 2017).

Thioredoxins (TRX), glutaredoxins (GRX), and glutathionylation are considered as protein thiols, which contain sulphydryl groups and are considered as protective and regulatory compounds for plant cell (Zagorchev et al. 2013). Different abiotic stresses raise both TRX and GRX in protein or gene level. Proteomics study of rice seedlings demonstrated the upregulation of responsible genes of TRX and GRX under Cu toxicity (Song et al. 2012). However, their function varies from stress to stress. Fatehi et al. (2012) reported that TRX activity increased by manyfold under salt stress in barley plant. On the other hand, amusingly, cold stress seemed to downregulate most TRX genes, but drought stress upregulated them, as a minimum at the earlier stages of the stress treatment (Nuruzzaman et al. 2012). Like TRX and GPX, the function of glutathionylation in a plant cell regarding abiotic stress tolerance is not so clear to date. Colville and Kranner (2010) reported that protein glutathionylation is a probable provider of defense mechanisms that confer desiccation stress tolerance.

10.8 Molecular Approaches in Regulating S Status in Plants

For growth and development, plants require a certain amount of sulfur. Due to the dynamic nature of the environment, plants may not get the exact amount of S as per requirement. Thus, plants have evolved with some strategies to control the S status in plants under diverse situations including S deficiency and unfavorable environmental condition (Table 10.3). From S uptake to assimilation into a metabolite, different regulatory factors tightly control the pathway to ensure proper concentration of S-containing compounds or inorganic SO_4^{2-} in cellular compartments essential for metabolic functions (Table 10.3). Understanding of molecular mechanism involved in S homeostasis allows us to engineer pathway in a way ensuring proper S level in plant even under environmental stress condition. Therefore, the study of transporter proteins, metabolites, and enzymes of the assimilatory pathway under S-deficient condition could be a pertinent approach to find out the regulatory factors of S metabolism. Under S deficiency, *Sultr1;1* expression is greatly enhanced, and *Sultr1;1* is more responsive to S status than *Sultr1;2* (Yoshimoto et al. 2002). To understand how the transporter proteins are controlled, different enzymes inhibitors were used: phosphatase inhibitors, OKA and CalyA, and kinase inhibitors, K252a. Phosphatase inhibitors, OKA and CalyA, inhibited the expression *Sultr1;1* under sulfur deficiency indicating the involvement of protein phosphatase in the

Table 10.3 Regulatory components of S metabolism and their function

Regulatory component in S metabolism	Target in S metabolic pathway	Mode of action	References
Sulfur-responsive element (SURE)	Present in promoter region of *Sultr;1*	Provide binding sequence 5 bp GAGAC for regulatory element	Maruyama-Nakashita et al. (2005)
SLIM1	*Sultr1;2* and Glucosinolates	Activate sulfate uptake and degrade glucosinolates	Maruyama-Nakashita et al. (2006)
Long hypocotyl 5 (HY5)	APS reductase (APR)	Control the APR gene expression	Lee et al. (2011)
MYB	APS reductase (APR)	Control the APR gene expression and regulated by SLIM1	Takahashi et al. (2011), Koprivova and Kopriva (2014)
miRNA395	ATP sulfurylases (APS) and *Sultr2;1*	Regulate APS expression and induced by SLIM1	Kawashima et al. (2009)
Cysteine synthase complex (CSC)	Cys	Modulate Cys biosynthesis	Wirtz et al. (2010)

regulation of *Sultr1;1* expression (Maruyama-Nakashita et al. 2004a). Further investigation revealed that among different phytohormones, only cytokinin could repress the *Sultr1;1* and *Sultr1;2* expressions in *Arabidopsis* indicating a role of cytokinin in S homeostasis in the plant (Maruyama-Nakashita et al. 2004b). Again, a sulfur-responsive element (SURE) was identified in 5′ promoter region of *Sultr1;1*. Furthermore, microarray analysis suggested that SURE is associated with some genes responsive to S deficiency (Maruyama-Nakashita et al. 2005). Another transcription factor, SLIM1, was reported to be involved in regulation of *Sultr1;2* expressions under S-limiting condition. Interestingly, SLIM1 itself was not affected by S concentration in the growing media. Also, there was no SLIM1 binding site in the sulfate transporters except *Sultr4;2* suggesting the presence of another factor that may connect the signaling between transporter genes and SLIM1 (Maruyama-Nakashita et al. 2006). A binding site for EIL group transcription factors was identified in the promoter region of *UP9C* gene in tobacco, a gene responsive to the sulfur limitation (Wawryzynska et al. 2010). Kasajima et al. (2007) suggested that *ASR1*, also known as *BIG* gene, is involved in sulfate metabolism pathway as the mutant *asr1-1* showed upregulation of SULTR2;2 and adenosine-5′-phosphosulfate reductase 1 (APR1) which was not affected by SLIM1. To investigate the transcriptional regulation of sulfate assimilatory genes, long hypocotyl 5 (HY5), a transcription factor, was reported to modulate APR expression. Unlike SURE and SLIM1, HY5 can bind to the promoter region of APR1 and APR2 but not in APR3 (Lee et al. 2011). However, APR expression is also regulated by MYB transcription factors (Yatusevich et al. 2010).

In some cases, gene expression is regulated posttranscriptionally by some RNA, microRNA (miRNA). These miRNAs bind with a protein to form RNA-induced silencing complex (RISC). The RISC then binds with mRNA complementary to miRNA. As a result target mRNA fails to be translated into protein. Sulfur deficiency in growth medium induces miRNA395 which in turn regulates the expression of *Sultr2;1* and *APS1* genes in the sulfur metabolic pathway. Interestingly, transcription factor SLIM1 can induce miRNA under sulfur limitation (Kawashima et al. 2009). The multienzyme complex formed by SAT and OAS-TL, known as cysteine synthase complex (CSC), is involved in sulfur homeostasis (Takahashi et al. 2011; Koprivova and Kopriva 2014). The CSC regulates Cys biosynthesis in different cell organelles and maintains SAT activity. However, S limitation induces accumulation of OAS which dissociates the complex (Droux et al. 1998; Wirtz et al. 2010). Still, there are not enough reports to elucidate the mechanism completely. Furthermore, regulatory networks of S metabolism could be investigated under abiotic stress condition which will allow us to answer the question how S is metabolized under adverse environment.

10.9 Conclusion and Future Perspectives

Although there are several reports on the role of S in plants under abiotic stress, the exact mechanisms and interactions are not revealed yet. Sulfur-associated amino acids (Met, Cys), iron-S-clusters, lipids, vitamins (biotin and thiamine), cofactors (CoA and S-adenosylmethionine), and peptides (such as GSH and PCs) play a significant role in abiotic stress tolerance. Molecular approaches to manipulate enzymes of S assimilation pathway such as ATP sulfurylase (ATP-S), APS kinase, PAPS reductase or APS reductase, sulfite reductase, serine acetyltransferase (SAT), and O-acetylserine/O-acetylhomoserine sulfhydrylase will widen the eyes view to exploit S as a more persuasive molecule in developing stress tolerance of plant (Anjum et al. 2015; Khan et al. 2016). Sulfur deficiency disrupts homeostasis of other essential nutrients, and thus the formation of basic structural components of the cell is hindered. A cross talk among GSH pools, miR395 levels, and ATP-S transcripts/activity regulates S pool and the pool of other essential nutrients within the plant which maintains the nutrient homeostasis for better plant development both under normal growth and abiotic stress condition (Anjum et al. 2015). This aspect should be considered for further studies.

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Chapter 11
The Role of Silicon in Plant Tolerance to Abiotic Stress

Tomasz Kleiber

Abstract Silicon (Si) belongs to the group of elements having a beneficial effect on plants. While it is not necessary for living processes, it may positively influence plant growth and yielding. The forms of Si which are easily available to plants and could be used in nutrition include potassium silicate, silica sol, slow-release Ca- and NH_4-silicates and choline-stabilised orthosilicic acid. Si supplementation may also significantly change the nutrient uptake by plants. The positive role of Si in plant growth is especially observed under stress conditions such as salinity, temperature (freezing, chilling), heavy metal toxicities (e.g. aluminium, cadmium, manganese) and drought. This chapter presents examples of the role of Si in plant nutrition, its role in abiotic stress tolerance to plants as well as the mechanisms of Si alleviation to various abiotic stresses in plants.

Keywords Silicon · Plants · Beneficial element · Abiotic stress

11.1 Introduction

Silicon (Si) is classified as a beneficial element for some plants. It means that under some environmental conditions, especially under stress pressure, it may positively influence plant growth and yielding. Liang et al. (2007) cited Epstein and Bloom (2005), who modified the generally accepted definition of essentiality of elements established by Arnon and Stout (1939). In their opinion an element is essential when it meets at least one of that criteria: (i) it is part of a molecule being an intrinsic component of the structure or metabolism of the plant, and (ii) the plant can be so severely deficient in the element that it shows abnormalities at various development phases in comparison to plants with a less deficient status of that element. Based on this definition, Si may be classified as an essential element for higher plants, which may soon be a universally accepted definition.

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11.2 Silicon Influence on Plant Physiology

11.2.1 Physiological Processes

In the opinion of Liang et al. (2003), silicon may be involved in physiological and metabolic processes and enhance structural activity in higher plants. Si supplementation of in vitro-cultured plants may promote beneficial physiological changes, such as better development of photosynthetic tissues and production of chlorophyll (Braga et al. 2009). Also in vivo an increased Si nutrition leads to positive changes such as chlorophyll quantity (*a*, *b* and *total*) in plants and changes in the transpiration rate (Schmidt et al. 1999; Dragišic Maksimović et al. 2007; Silva Lobato et al. 2013). Studies showed that Si reduces the transpiration rate (Agarie et al. 1998), increases photosynthetic capacity or stimulates antioxidant superoxide dismutase activity (Schmidt et al. 1999). Si may also influence processes taking place in plant tissues, e.g. condensation of their structure or lignin synthesis (Zhao et al. 2013). According to Dragišic Maksimović et al. (2007), at the level of plant parts (especially in the case of leaves), Si may also modulate the metabolism and utilisation of phenolic compounds, which is likely the consequence of the formation of Si-polyphenol complexes. Positive symptoms of Si application have also been reported by Gunes et al. (2007a) and Sacała (2009) in connection with such physiological parameters as photosynthesis or stomatal conductance. Si treatment significantly influences the plant water status (described as RWC – relative water content) (Kleiber et al. 2015a) and reduces transpiration rates compared with combinations without Si treatment. Liang et al. (1996) claimed that Si treatment by improving plant growth enhances root activity and photosynthesis. Another important aspect is connected with an alleviation effect of osmotic stress by reducing transpiration and/or improving retention of water.

Generally Si content in plant tissues could be genotype varied, according to Ma and Takahashi (2002), reaching as much as 10.0% of dry weight. In plant tissues, about 99% of Si is found in the silic form and only <1% as a colloidal or ionic, soluble form (Ma et al. 2001). Until recently literature on the subject disregarded the role of Si, even though most plants take root in the environment rich in silicates but poor in its forms readily available to plants (Epstein 1999; Richmond and Sussman 2003). Graminaceous plants typically absorb higher amounts of Si compared with others. In turn, most dicotyledonous plants passively absorb Si, although some dicots, such as legumes, exclude Si uptake (Ma et al. 2001; Liang et al. 2005; Sacała 2009). Si is available and readily absorbed as uncharged silicic acid $[Si(OH)_4]$ and is ultimately irreversibly precipitated throughout the plant as amorphous silica. Mitani and Ma (2005) claimed that in rice plants, a higher density of the transporter for radial transport and the presence of a transporter for xylem loading are responsible for the high Si accumulation. Nevertheless, the effect of Si nutrition on some species (e.g. lettuce) could be weaker than in other plants (Voogt and Sonneveld 2001). Ma and Yamaji (2006) divided plants into three groups depending on the Si transport and accumulation: high (e.g. rice), medium (e.g. cucumber) and low (e.g.

tomato). In rice the uptake and transport of Si are an active process (Epstein 1994; Ma et al. 2006), while some dicots (e.g. cucumber, melon, soybean or strawberry) take it up passively (Takahashi et al. 1990; Ma et al. 2001; Mitani and Ma 2005).

Different forms of Si are available for plants, e.g. Ca- and NH_4-silicates (Górecki and Danielski-Busch 2009), orthosilicic acid (Dragišic Maksimović et al. 2007), potassium silicate (Lee et al. 2000; Iwasaki et al. 2002a), silica sol (Jarosz 2013) and sodium silicate (Rogalla and Römheld 2002). Also ch-OSA (choline-stabilised orthosilicic acid) may be used in plant nutrition (Kleiber 2014b; Kleiber et al. 2015b). ch-OSA is a bioavailable Si form for humans (the decision of the European Food Safety Authority 2009) and may be used for therapeutic purposes. Studies have shown that a combined application of ch-OSA + Ca/Vit D3 had a potential beneficial effect on bone collagen compared to Ca/Vit D3 alone. This suggests that such therapy could be potentially applied/used in osteoporosis (Spector et al. 2008).

A particularly important role of Si nutrition is observed in the case of soilless cultures, since plants are not capable of orthosilicate uptake directly from the soil, in which they are naturally found (Datnoff et al. 2001). Among other things, Si may affect plant growth, habit and yielding. In the opinion of Liang et al. (2007), recent findings suggest that Si is not inert but plays a role in a physical or mechanical barrier in plants. It is not only deposited in the cell walls but participates in metabolic and/or physiological activities, especially in plant response to varied stresses. The positive role of Si in the photosynthetic activity was, for example, studied in heavy metal stress (Kleiber et al. 2015b), UV radiation (Li et al. 2004; Shen et al. 2010), water deficit (Gong et al. 2005) or pest infestation and pesticide application (Richmond and Sussman 2003). Si is also considered a desirable element, stimulating yielding and resistance to disease in certain plants (Epstein 1999; Datnoff and Rodrigues 2005; Fauteux et al. 2005). Liang et al. (2007) stated that further studies are needed to investigate the effect of Si in alleviation of various stresses. The direction adopted in present-day plant breeding should be to produce genetic modifications in plants to enhance their potential for Si uptake to such amounts that plants may overcome the stresses they are exposed to during culture (Ma and Yamaji 2006).

11.2.2 Influence on Nutrient Uptake

Because of its effect on uptake of other nutrients, Si may alleviate various stresses, as well as improve yielding of plants (Epstein 1999; Aziz et al. 2002; Jarosz 2013). The currently confirmed effect of Si on the uptake of other nutrients varies greatly and is multifaceted. Incorporation of Si in plant nutrition programmes may improve utilisation of nutrients (Epstein 1994). Moreover, Si promotes nitrogen (N) metabolism (Watanabe et al. 2001) and promotes and enhances uptake of phosphorus (P) while at the same time reducing uptake of iron (Fe) and Mn (Kozik and Komosa 2012). In cadmium (Cd) stress, the Si treatment may increase calcium (Ca) uptake by plants (Song et al. 2009). Meanwhile Ma and Takahashi (1993) claimed that Si nutrition may decrease Ca content in the shoots of plants, which could be a result of a decreasing transpiration rate caused by Si. Many studies have shown a positive Si effect on a more effective utilisation of P and potassium (K) (Lee et al. 2000; Farshidi et al. 2012; Kleiber 2014b; Jarosz 2015; Kleiber et al. 2015a). In the case of microelements, Jarosz (2013) stated that Si has no major influence on the content of Fe in cucumber leaves. In contrast, the effect of Si on the Mn and Zn status of plants may be varied (Horiguchi 1988; Lee et al. 2000; Jarosz 2013; Kleiber 2014a). In turn, Si application may influence the status of some metallic microelements (Fe, Mn and Zn) and accumulation of metal-mobilising compounds in micronutrient-deficient plants (Bityutskii et al. 2014). Research results have shown that Si treatment significantly increases Fe status in leaves of plants deprived of Fe, whereas the status of other microelements is not affected by Si. The above-mentioned authors suggested that the major alleviating effect of Si could be connected with the enhancement of Fe distribution towards juvenile parts of shoots, along with the accumulation of Fe-mobilising compounds such as catechin (in roots) or citrate (in leaves/roots).

11.2.3 Response of Plants Under Heavy Metal Stress

One of the most extensively scientifically documented applications of Si is the alleviation of heavy metal stress. Excessive uptake of heavy metals, e.g. Mn, causes a strong oxidative stress in plants and as a consequence results in a deterioration of their yielding or the development of toxicity symptoms (Kleiber 2014a; Kleiber et al. 2014). Earliest studies stated a significant and important role of Si in the alleviation of the toxic effects of Mn (Horiguchi 1988; Iwasaki et al. 2002a, b; Dragišic Maksimović et al. 2007; Liang et al. 2007; Zanão Júnior et al. 2010), Al (Hiradate et al. 1998) or Cd (Shi et al. 2010; Zhang et al. 2008; Wu et al. 2016; Hasanuzzaman et al. 2017). Previous studies on the use of Si in relieving metal stress were conducted on various species, e.g. barley, beans, cowpea, cucumber or rice.

The key mechanisms for Si alleviation of abiotic stresses in higher plants include (Liang et al. 2007) (1) antioxidant system stimulation, (2) complexation or co-precipitation of toxic metal ions with Si, (3) immobilisation of those ions in the growing medium and (4) uptake and translocation within plants. In the case of environmental stresses, Si prevents cell membrane damage, while in the form of the orthosilicic acid, it may induce defence response, activate signal proteins and contribute to the production of stress hormones in fungal diseases (Agarie et al. 1998; Fauteux et al. 2005; Hasanuzzaman et al. 2017, 2018). Alleviation of chemical stress may be related to the induction of antioxidant response and the protection of membranes that increases plant tolerance to damage (Gunes et al. 2007b).

Spectacular and positive symptoms of Si treatment under heavy metal stress include an increase in the net photosynthesis rate (P_N) (Kleiber et al. 2015b) or biomass production (Dragišic Maksimović et al. 2007, 2012), for example, increasing ch-OSA concentrations (0.21–0.63 mg Si dm^{-3}) in hydroponic culture of lettuce significantly improved yielding of plants grown under Mn stress (Kleiber 2014b). In leaves of hydroponically grown cucumber (*Cucumis sativus* L.) exposed to high Mn nutrition, it induced both growth inhibition of the whole plant and caused visual Mn toxicity symptoms (Dragišic Maksimović et al. 2007). Although the Mn status of leaves did not differ between plants exposed to varied Si treatments, symptoms of this heavy metal toxicity were not observed in plants fed with Si. However, opinions on the Si effect on Mn content in plants vary considerably: some authors (Iwasaki et al. 2002a; Führs et al. 2009; Kleiber 2014b) suggested a lack of influence of Si on Mn content in plants, while others (Horiguchi 1988; Jarosz 2015) claimed that Si reduces the Mn content in plant leaves. In turn, Zanão Júnior et al. (2010) found that Si application in hydroponic caused a decrease of Mn concentration in leaves, which was related with an increasing content of that metal in roots, thanks to which the toxicity was reduced. The positive role of Si in the alleviation of Mn stress caused by an elevated production of hydroxyl radicals ($^{\cdot}$OH) in the leaf apoplasts of hydroponically grown cucumber (*Cucumis sativus* L.) with optimal (0.5 μM) or toxic (100 μM) Mn levels in the nutrient solution and also with/without Si supplementation was studied by Dragišic Maksimović et al. (2012). Si addition decreased the apoplastic concentration of free manganese ($^{2+}$) and hydrogen peroxide in toxic Mn-treated plants. In Mn stress Si treatment suppressed the Mn-induced increased abundance of peroxidase (POD) isoforms in the leaf apoplastic fluid and led to a rapid suppression of guaiacol-POD activity. While Si application reduced the OH accumulation in the leaf apoplasts with excessive Mn, adding Si to the Mn($^{2+}$)/H^{2}O^2 reaction mixture did not directly affect the Fenton reaction (in vitro). The above-mentioned authors found that Si contributes indirectly to OH decrease in the leaf apoplasts by decreasing the free apoplastic Mn($^{2+}$), thus regulating the respective reaction. In vitro a direct Si inhibitory effect on guaiacol-POD activity may contribute to a reduction of the POD-mediated $^{\cdot}$OH generation. Si may oxidise Mn mediated by POD through an interaction of phenolic compounds in the solution phase of the apoplast, maintaining the apoplast in a reduced state, which is thought to be necessary for improved Mn leaf tolerance (Iwasaki et al. 2002a, b).

Iwasaki and Matsumura (1999) found that the alleviation effect of Si on pumpkin (*Cucurbita moschata* Duch cv. Shintosa) cultivated under excessive Mn nutrition was cultivar-dependent and positively correlated with Si nutrition. In their opinion Si alleviated the Mn toxicity through a localised Mn accumulation with Si in a metabolically inactive form around the base of the trichomes on the leaf surface. In rice Si content in the top parts of Si+ plants (50 ppm SiO$_2$) is higher compared with the control plants (Si-) regardless of Mn nutrition (within the range from 0.32 to 100 ppm Mn) (Horiguchi 1988). Also transpiration rates in plants with no Si treatment were higher independently on their Mn status. In the case of higher Mn nutrition, the increase of Mn root concentration caused by Si was less evident than the decrease in Mn content in the tops of plants. Peroxidase activities in plants increased with Mn nutrition; nevertheless, the peroxidase activity in the case of Si+ plants was lower comparing with the control plants (Si-). Si enhances the internal tolerance to Mn toxicity with a simultaneous decrease of Mn concentration in plants (Horiguchi 1988). Si reduces the Mn concentration in the symplasts (<10%) and leads to a greater concentration of Mn bound to the cell walls (>90%) when compared with the control plants (≈50% in each compartment), making Mn less available and less toxic (Rogalla and Römheld 2002). In the case of cowpea, Horst et al. (1999) found that Si reduced the Mn apoplastic concentration and may modify the cation sorption capacity of the cell wall. It seems that the interaction of Si and metals reduces the activity of toxic metal ions in the medium (Hiradate et al. 1998).

Si can increase plant tolerance to Cd in the case of monocotyledonous and dicotyledonous species and reduce the toxicity symptoms of that heavy metal (Neumann and zur Nieden 2001; Shi et al. 2005b; Feng et al. 2009; Song et al. 2009). Shi et al. (2010) studied the effect of Si supplementation in two peanut (*Arachis hypogaea* L.) cvs. ('Luhua 11' and 'Luzi 101') differing in Cd tolerance. Cd decreased plant growth and caused oxidative stress in both cultivars, but the response was cultivar-dependent. The Si-promoted alleviation effect on that heavy metal was related, for example, with the reduction of Cd concentration in shoots (in the seedling phase). The response of plants to Si+ under Cd stress varied between the cultivars: in cv. Luhua 11, Si reduced transport of that heavy metal to aboveground parts of plants (shoots and leaves), and increased enzyme activities (CAT, POD and SOD) in roots could reduce Cd toxicity. In the other cultivar, Si stimulated antioxidant systems and decreased Cd concentration in shoots. In the opinion of Zhang et al. (2008), Si treatment reduced Cd accumulation in shoots of rice by compartmentalisation of Cd in the root cell walls. The Si application in hydroponic cultivation of flowering Chinese cabbage (*Brassica campestris* L. ssp. chinensis var. utilis) reduced Cd stress (Wu et al. 2016) by decreasing Cd shoot concentrations as well as its translocation factor, though the concentrations of that heavy metal in roots and the total uptake showed an upwards trend. Song et al. (2009) also confirmed that Si nutrition alleviated the heavy metal stress (Cd) by reduction of its uptake.

Si significantly alleviated Al toxicity in barley (*Hordeum vulgare* L.) plants (Hammond et al. 1995) – Si improved root growth, which was related with reducting Al uptake by roots. The possible mechanism of the Si alleviation effect on that toxicity could be related with interactions between ions reducing the activity of heavy metal ions in the growing medium (Hiradate et al. 1998). Baylis et al. (1994) confirmed the positive effect of Si treatment but emphasised the importance of the pH level. It is possible that the precipitation of subcolloidal, inert hydroxyaluminosilicate could be responsible for the diminished concentration (activity) of phytotoxic Al in the hydroponic culture. In corn (*Zea mays* L.), Ma et al. (1997) found that in plants grown under Al stress, the Si application provided protection against the inhibition of root elongation. It was also concluded that the formation of Al-Si complexes was responsible for alleviation of Al toxicity. In the opinion of Cocker et al. (1998), a possible mechanism of Al toxicity alleviation is connected with the formation of sparsely soluble aluminosilicates or hydroxyaluminosilicates (or both) within the root cell wall (apoplastic) space, thereby reducing the concentration of free, toxic Al^{3+} ions. Barcelo et al. (1993) found that teosinte (*Zea mays* L. ssp. mexicana) plants exposed to Al (60 mM/120 mM) were less inhibited in their growth when Si was added to the solution (4 mM Si) – the mechanism was attributed mainly to the inhibitory effect of Al uptake. After Si treatment higher concentrations of organic acids (malic and formic) were determined in the plants. Possibly Si may have additional roles in Al toxicity by mediating the metabolism of phenolic compounds, as it has been reported that Si+-treated maize plants release 15 times more phenolics than control plants (Si-) (Kidd et al. 2001). Catechin and quercetin or other flavonoid phenolics have a strong Al-chelating potential and may provide metal tolerance in plants.

Several hypotheses have been presented to explain the mechanisms of the Si effect in the inhibition of heavy metal ion uptake, e.g. by binding heavy metal ions in the substrate by compounds, which the plant is not capable of absorbing, by binding cations in cell walls, stimulating antioxidants and enzymes reducing the adverse effects and by binding ions in the cytoplasm and next transporting them to the vacuoles (Hiradate et al. 1998; Pilon-Smits et al. 2009). Si influences the metabolic/physiological changes in plants (Liang 1999). Neumann and zur Nieden (2001) and Shi et al. (2005a) claimed that it stimulates the plant's antioxidant defence. In the opinion of Liang et al. (2007), Si reduces lipid peroxidation and improves plasma membrane and tonoplast structure, integrity as well as vital functions. The following factors take part in the mechanism of the Si-enhanced Mn tolerance: (1) decrease the Mn concentration in apoplasts through an improved adsorption of that microelement on the cell walls and (2) an alleviation of Mn toxicity facilitated through increased solubility of Si concentrations in the apoplasts (Iwasaki et al. 2002a). According to Wu et al. (2016), the potential mechanisms of reducing Cd translocation may include (1) decreasing Cd content and proportions in symplast/apoplast saps (Nwugo and Huerta 2008; Ye et al. 2012) and delaying metaxylem development in roots under low heavy metal stress (Vaculík et al. 2012) as well as enhanced formation of complexes with acids (both organic or inorganic) and reducing translocation to aboveground parts of plants (Collin et al. 2014; Keller et al. 2015).

11.2.4 Response of Plants Under Water Stress

According to Sacała (2009), water availability in soil is one of the major environmental factors limiting the growth and yielding of crops. Water stress may result from a real water deficit in the soil (drought) or excessive salinity of the root zone. Current studies on the use of Si in drought stress relief are particularly important for different cereal species. Drought is the source of abiotic stress, which reduces growth and development rates, causes flower aborting and decreases crop yields (Showemimo and Olarewaju 2007) while also deteriorating photosynthetic parameters, root development and water potential.

Under optimal water conditions, Si treatment had no effect on growth and physiological parameters of rice cultivars (*Oryza sativa* L.) (Chen et al. 2011). However, under water stress, it affected negatively plant growth parameters, e.g. dry weight, root traits, water potential and selected photosynthetic parameters such as F(v)/F(0), basal quantum yield, and F(v)/F(m) maximum quantum efficiency of PSII photochemistry. Under Si treatment positive symptoms were found in plant physiology, such as increased photosynthetic rate (Pn), transpiration rate (Tr) and the above-mentioned other physiological parameters. Those authors claimed that water stress influences the nutrient status of plants, as it increases concentrations of K, Na, Ca, Mg and Fe, while Si significantly reduces the concentration of these nutrients. These results suggested that Si treatment of rice plants was useful in increasing drought resistance through an improvement of the nutrient status as well as enhancement of photochemical efficiency.

Kaya et al. (2006) conducted experiments with another important cereal species – maize (*Zea mays* cv. DK 647 F_1). The effect of Si treatment on the response of plants was investigated under varied water conditions: optimal and with strong water deficit. Induced drought stress reduced the total dry matter, relative water content and chlorophyll content with a simultaneous increase in proline accumulation and electrolyte leakage in plants. Si improved the physiological response, but generally the levels remained significantly lower than in the control (except for electrolyte leakage and root-shoot ratios). Kaya et al. (2006), similarly as Chen et al. (2011), found an effect of Si on the chemical composition of water-stressed plants. The Si status of plants was correlated with Si content in the nutrient solution. Water deficit decreased the K and Ca contents, whereas Si treatment increased them. In conclusion, the Si nutrition may be one approach to improve growth of this crop and increase its production under dry conditions but may not be a full substitute for an adequate water supply.

Differences have been reported in SOD and POD activity between different Si treatments of wheat (*Triticum aestivum* L.) grown under drought stress at different developmental stages (Gong et al. 2008). The Si treatment did not influence the contents of total soluble protein and protein carbonyl or H_2O_2, while at the filling stage, it decreased the content of H_2O_2 and protein carbonyl and increased content of total soluble protein. Additionally, a downwards trend was also observed for the content of TBARS (thiobarbituric acid reactive substances) and the activities of acid phospholipase (AP) and lipoxygenase (LOX) under dry conditions.

Si limited the decrease in dry weight under water stress conditions but had no effect on DM production under wet conditions in plants of sorghum (*Sorghum bicolor* (L.) Moench) (Hattori et al. 2005). Under drought conditions Si+ plants were characterised by a lower shoot-root ratio, indicating the facilitation of root growth and the maintenance of the photosynthetic rate and stomatal conductance at a higher level when compared with the control (Si-). Those authors stated that the diurnal determination of the transpiration rate indicated that the Si treatment plants could uptake more water from dry soil and maintain a higher stomatal conductance. In the opinion of those authors, Si application may be useful in improving drought tolerance of sorghum thanks, to improved water uptake.

The effect of Si on potato (*Solanum tuberosum* L.) response under drought stress was investigated in studies conducted by Crusciol et al. (2009). Si treatment and water deficit resulted in an increased Si concentration in leaves with a simultaneous increase of proline concentrations. In the opinion of those authors, Si may be associated with plant osmotic adjustment. That factor decreased total sugar/soluble protein concentrations in the leaves. Si nutrition reduced stalk lodging and increased mean tuber weight and, consequently, tuber yield, especially under water deficit. Similarly to agricultural crops, also horticultural species exhibit a positive response to Si nutrition. Strawberry plants (*Fragaria ananasa* Duch. cv. Elvira) at the foliar application of potassium-silicate alkaline utilised water more efficiently in the process of photosynthesis, as a result improving their water relations and significantly reducing water losses from transpiration (Mikiciuk and Mikiciuk 2009).

11.2.5 Response of Plants Under Salinity Stress

In today's world increasingly frequent problems are connected with excessive salinity of soil and water. One way to limit them is to use Si nutrition. Previous studies focusing on that issue were conducted on various species, e.g. barley (Liang et al. 1996, 2003; Liang and Ding 2002), rice (Matoh et al. 1986; Yeo et al. 1999), wheat (Ahmad et al. 1992), tomato (Al-Aghabary et al. 2004) or cucumber (Zhu et al. 2004).

In a study by Liang (1999), plants of barley (*Hordeum vulgare* L.) treated with Si were characterised by increased SOD activity in leaves and HC-ATPase activity in roots, while malondialdehyde (MDA) concentration in leaves decreased significantly when compared with the control plants (Si-). In turn, Yeo et al. (1999) and Romero-Aranda et al. (2006) found that Si treatment under salinity stress increased the stomatal conductance in tomato and rice, respectively.

Matoh et al. (1986) studied the effect of Si treatment in hydroponically grown rice under salinity stress with the presence of either NaCI, sea water or polyethylene glycol (PEG) at an osmotic potential of up to 186 mOsmol/kg, equivalent to 100 mM NaCI or 20% sea water. The most detrimental factor was NaCI, followed by sea water and PEG. The chemical composition of plants (N, P, K and Ca concentrations) was comparable in the studied combinations. A lack of an Si source brought about a more severe growth reduction in rice plants subjected to 100 mM NaCI stress. In the Si+ plants, the Na contents in the shoots were nearly half of those in the shoots of Si- plants. Savvas et al. (2007) clearly indicated that Si is capable of suppressing the uptake and translocation of Na and Cl to the photosynthetically active leaves of roses under high external NaCl salinity. Also salt tolerance of wheat (*Triticum aestivum*) or barley could be improved by an addition of small amounts of the soluble Si form (Ahmad et al. 1992; Liang et al. 1996). Obviously, plant response is connected with the element uptake. Moderate salinity (50 mmol•dm^{-3}) leads to increased H_2O_2 levels in cucumber leaves, membrane peroxidation and increased electrolyte efflux. Si decreases salt-induced production of H_2O_2 and improves photosynthesis rates (Al-Aghabary et al. 2004). A similar phenomenon was found by Gunes et al. (2007a) in spinach grown under B toxicity, which was alleviated by Si nutrition. Si addition to the nutrient solution (1 mmol dm^{-3} K_2SiO_3) significantly alleviated the salinity stress (Zhu et al. 2004).

Studies have shown that Na concentration in the shoots decreased under Si treatment (Matoh et al. 1986; Yeo et al. 1999; Liang et al. 1996; Liang 1999). Haghighi and Pessarakli (2013) conducted experiments investing the influence of Si and the Si nanoparticle (N-Si) on salinity tolerance (at 0, 25 and 50 mM NaCl) of cherry tomatoes (*S. lycopersicum*) at an early growth stage. Varied Si and N-Si concentrations were tested (0, 1 and 2 mM). Under the Si and N-Si treatment and addition of NaCl to the nutrient solutions, plants were grown up to 42 days. Salinity adversely affected plant development (fresh/dry weights, root volume and stem diameters), while it also decreased substomatal CO_2, photosynthetic rate, mesophyll conductance and photosynthetic water use efficiency. Si improved the fresh and dry weights of plants, root volume and chlorophyll concentration. Both Si and N-Si treatments improved the photosynthetic rate, mesophyll conductance and plant water use efficiency under NaCl stress.

Liang et al. (1996) stated that Si may decrease permeability of the plasma membrane in leaf cells, while it simultaneously significantly improved the ultrastructure of chloroplasts damaged by NaCl with the double membranes disappearing and the grannae being disintegrated in the Si- plants. Generally the leaf membrane stability index decreased with an increase in salinity levels (Haghighi and Pessarakli 2013). High salinity increased membrane permeability in sensitive rice varieties, strawberry and wheat (Lutts et al. 1996; Kaya et al. 2003; Levent Tuna et al. 2008). Levent Tuna et al. (2008) claimed that at the Si treatment under salinity stress, membrane permeability is partially maintained the same as under nonsaline conditions. Based on the current knowledge, Liang et al. (2007) suggested that possible mechanisms underlying Si-enhanced salinity tolerance are among others those connected with increased ATPase and PPase activities and simultaneous decrease of Na and an increase of K uptake. It results in reduced osmotic stress of plants. Another positive effect is also connected with increasing root activities and enhanced nutrient uptake, which leads to an improved nutrient balance. Si also influences enzymatic processes, e.g. SOD, POD, CAT and glutathione reductase (GR) activities (Liang et al. 1996, 2003; Liang 1999). Also other authors (Al-Aghabary et al. 2004; Zhu et al. 2004) confirmed the hypothesis concerning the Si role in lipid peroxidation in salt-stressed plants by enhancing the activity of antioxidant enzymes and non-enzymatic antioxidants (Liang 1999; Liang et al. 2003).

11.3 Conclusion

Although silicon is one of the most commonly occurring elements on Earth, its availability to plants under natural conditions is relatively low. This chapter presented the influence of silicon treatment on various aspects of plant physiology and their nutritional status. The discussed papers presented the possibility of using silicon to alleviate various abiotic stresses: salinity, heavy metals and drought. Silicon also affects the reaction of plants under biotic stress. Certainly, further research needs to be conducted to find other forms of silicon available for plants, as well as confirm silicon applicability in integrated plant production programmes, aimed at reducing the consumption of plant protection products, which is important for the health of consumers.

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Chapter 12
Mechanisms of Selenium-Induced Enhancement of Abiotic Stress Tolerance in Plants

Barbara Hawrylak-Nowak, Mirza Hasanuzzaman, and Renata Matraszek-Gawron

Abstract Selenium (Se), an essential micronutrient for humans, animals, and some microorganisms, has been found to be a beneficial trace element for many plant species, especially Se hyperaccumulators. Selenium accumulation in plants profoundly affects many biochemical reactions in cells. There is a growing interest in understanding the plant reaction to Se enrichment, both to ensure adequate dietary Se intakes for humans and animals, which often needs Se biofortification using edible crops, and to achieve increased tolerance of plants to some environmental stress. In recent years, many investigations have shown that Se-enriched plants exhibited enhanced tolerance to some abiotic stresses, e.g. cold, high temperature, drought, salinity, UV radiation, and excess of some trace metals/metalloids. In plants exposed to environmental stresses, the protective role of Se ions, used in relatively low concentrations, has often been attributed to stimulation of antioxidative protection systems, but the associated mechanisms are complicated and not fully elucidated. To obtain positive effects of Se phytofortification, the possibility of accumulation of this element in given plant species, the chemical form of Se applied, the way of the application thereof, as well as the probability of its interaction with other elements should be taken under consideration. In this chapter, we will focus on reviewing the effects of Se biofortification on plants growing under different abiotic stress conditions. Changes in the physiological and biochemical characteristics of Se-supplied plants, with particular emphasis on the influence of Se on the changes in enzymatic and non-enzymatic antioxidant defence mechanisms under abiotic stress, will be summarised in this review.

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Keywords Trace element · Plant nutrient · Fortification · Reactive oxygen species · Plant growth

12.1 Introduction

Selenium (Se), a metalloid mineral nutrient, plays a fascinating and still not fully understood role in the metabolism and function of organisms. The perception of Se has undergone considerable changes over the last decades. While its toxic influence was identified during the 1930s causing loss of hair and hoof in animals, its essential function in the metabolism of animals, humans, and microorganisms was recognised later, i.e. with the finding that Se deficiency caused 'white muscle disease' in feedstock in the 1950s. Its essentiality in animal and human organisms was accepted after the establishment of selenocysteine (SeCys) as the 21st essential amino acid (Lenz and Lens 2009). Afterwards, the studies on Se progressed rapidly using of tools from molecular biology, genetics, and immunology. Selenium is now known to be a very important micronutrient for proper functioning of humans, animals, archaea, and some other microorganisms as a structural component of so-called selenoproteins (El-Ramady et al. 2016). This element may play a number of biological roles, ranging from protection against cancer to influence on hormone metabolism. Many epidemiological studies have confirmed that Se deficiency in the diet increases the incidence of cardiovascular diseases, leads to thyroid gland dysfunction, and impairs the function of the immune and nervous systems (Rayman 2000). According to Hamilton (2004), Se has three levels of biological activity: (1) trace concentrations are essential for proper growth and development; (2) moderate concentrations can be stored to preserve homeostatic functions; and (3) high concentrations can cause toxic effects. Since both insufficient or excessive Se intake may have serious consequences for human health, this micronutrient is often described as a 'double-edged sword' (Hawrylak-Nowak et al. 2015).

Food is the main source of Se for humans and animals. Several different strategies may improve the suboptimal Se status, including a diversified diet, dietary supplements, fortification of food products, and biofortification (Malagoli et al. 2015). In recent years, there has been an increasing demand for foods with a targeted, desired effect on the organism, i.e. the so-called functional foods. Inclusion of this type of food in the diet may limit the risk of development of some diseases. One of the methods for acquisition of functional food is the process of plant biofortification (phytofortification) with easily absorbable minerals, e.g. Se (Nestel et al. 2006: White and Broadley 2009). Unlike to many other organisms, Se has not been revealed to be an essential element for growth and development of flowering plants (angiosperms). Nevertheless, the results of research conducted in recent years allowed to include Se in the group of beneficial elements (Kopsell and Kopsell 2007: White 2016). Selenium was classified as a quasi-essential micronutrient or beneficial element for many plant species, especially Se hyperaccumulators, which can achieve twofold higher biomass in the presence of Se (El-Ramady et al. 2016), and found to play a positive role in the resistance of many plant species to both abiotic (Hasanuzzaman et al. 2010; Feng et al. 2013: Sieprawska et al. 2015 and references therein) and biotic (Mechora and Ugrinović 2015) stresses. On the other hand, excess of Se can be very toxic to all organisms (White 2016).

Selenium has properties that make it a unique element in relation to other metals or metalloids. It can occur in both inorganic and organic chemical forms, which are characterised by differentiated availability, bioaccumulation, and toxicity, and it is an essential element for most organisms (El-Ramady et al. 2016). Selenium is a chemical analogue of sulphur (S), and therefore it is taken up and accumulated to some extent by all plant species. The plant Se levels occurring in nature or in crops strictly depend on Se content in the soil, soil properties, and the concentration of antagonistic S compounds (Malagoli et al. 2015). Selenate (Se^{6+}; SeO_4^{2-}) is the main water-soluble chemical form of Se found in oxygenated soils, i.e. most cultivated soils, while selenite (Se^{4+}; SeO_3^{2-}) dominates in anaerobic soils with an acidic to neutral pH, such as paddy soils. In the soil solution, Se^{6+} ions are rather mobile, but Se^{4+} ions are strongly absorbed by aluminium and iron hydroxides/oxides and, to some extent, by organic matter and clays. Therefore, the application of selenates to soils enables immediate uptake of Se ions by roots, whereas selenite addition provides a longer-lasting Se fertiliser (White 2016). Plant roots can also take up organic Se compounds, such as SeCys and selenomethionine (SeMet), but are unable to absorb elemental Se or metal selenides (White and Broadley 2009). The current methods to apply Se-containing fertilisers as a foliar spray or soil fertiliser have been used to increase the Se content in the edible parts of plants and to obtain Se-biofortified crops. The biofortification of plants with Se often can simultaneously prevent the damage caused by various environmental stresses (Feng et al. 2013; Malagoli et al. 2015).

According to Lynch (2007), nowadays we need a ‘second’ green revolution to increase the yielding of crop plants grown in low-fertility soils (or under adverse environmental conditions). Similar as the previous green revolution was based on crops reacting positively to high soil fertility, the ‘second’ green revolution should be based on crops tolerant to low soil fertility or more resistant to other abiotic stresses. Thus, the increase in the tolerance of crop plants to adverse environmental factors resulting from biofortification of their biomass with Se can be a part of this trend and may bring significant economic benefits in the future that are associated with, for example, management of areas where crop production with traditional cultivation methods is highly difficult. Besides the benefits associated with the increase in plant resistance to stress factors, an additional positive effect will be reflected in production of Se-enriched plants. Their biomass can be used for consumption, particularly in regions characterised by deficiency of dietary Se, e.g. in many European and Asian countries (Oldfield 2002). Moreover, some studies have shown that plants supplied with Se can modify their secondary metabolism and their biomass can be richer in some health promoting phytocompounds (Malagoli et al. 2015).

In recent years, numerous papers have been published dealing with Se as an effective phytoprotectant counteracting negative effects of various stresses (see reviews by Hasanuzzaman et al. 2010; Feng et al. 2013; Sieprawska et al. 2015). Oxidative stress is a consequence of both biotic and abiotic stress factors. This stress is provoked by a serious cell imbalance between the generation of reactive oxygen species (ROS), including $O_2^{\bullet-}$, $^{\bullet}OH$, and H_2O_2, and enzymatic and non-enzymatic antioxidants, which leads to dramatic physiological disorders (Lin et al. 2012). Either directly or indirectly, Se can influence the generation and quenching of ROS that are overproduced under stress conditions. This phenomenon may be a crucial mechanism for mitigation of negative consequences of abiotic stress in plants (Feng et al. 2013). Besides, the recent proteomics analysis performed by Wang et al. (2012) revealed that proteins involved in photosynthesis in leaves, as well as carbohydrate and protein metabolism in roots, were upregulated at low Se doses under which the growth of plants was also promoted. Although the protective role of low Se concentrations in stressed plants has been attributed to regulation/activation of antioxidative defence systems, in fact, the ability of Se to ameliorate the adverse effects of various abiotic stresses can be related also to several alternative mechanisms that are discussed in the next sections. Notwithstanding, in spite of its various positive effects in plants, Se has been denied the status of essentiality. The beneficial influence of Se on plants suggests a possibility of using this element as a factor that potentially enhances crop resistance to abiotic stresses, which are a major global problem affecting increasing areas of arable soils in the conditions of the dynamic climate changes occurring over the recent decades.

12.2 Selenium: A Key Regulator of Abiotic Stress Tolerance

Although Se is an essential trace element for human and animals, its essentiality is still unconfirmed in plants. It has been 60 years when the beneficial effect of Se was first reported by Schwarz and Foltz (1957). Previously Se was regarded as a toxic metalloid, but at low concentration, it showed beneficial effect in many plant species. The physiological basis of Se-induced stress tolerance was first revealed when it was found to form part of the important antioxidant enzyme, GPX (Rotruck et al. 1973). In the last couple of decades, a plenty of research works has been conducted to know the role of Se in plants. Numerous plant studies have revealed that Se not only improves the growth of plants but protects them from various abiotic stresses. In recent years, the physiological mechanisms of Se-induced abiotic stress tolerance have been studied. The major effects of Se towards abiotic stress tolerance are the improvement of photosynthesis, antioxidant defence, and higher uptake of water and nutrients. In *Zea mays*, low dose of Se (1 μM) provided increase in net photosynthetic rate and maintained chloroplast ultrastructure during salt stress (Jiang et al. 2017). Exogenous Se also regulated ion homeostasis in plants and protected them from salt stress. According to Feng et al. (2013), ‘Se may enhance the nutrient uptake and distribution to plant cells, maintain ion homeostasis and upregulate

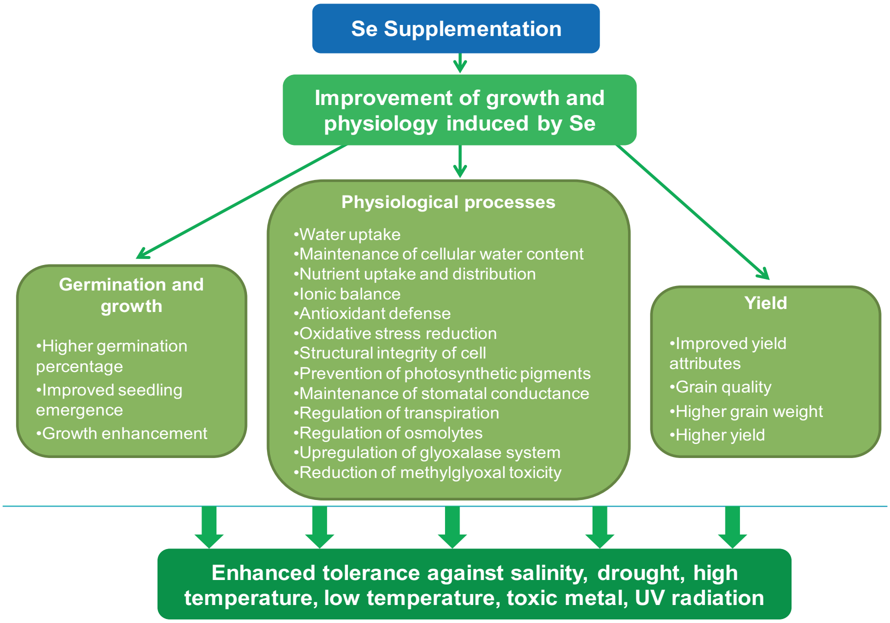

Fig. 12.1 Multiple functions of Se towards plant abiotic stress tolerance

antioxidant defense'. In fact the role of Se in regulating the antioxidant defence has been widely studied in the last couple of decades. In our study, we found that Se provided coordinated upregulation of both antioxidant and glyoxalase systems in conferring plants' tolerance to drought, salt cadmium, and high temperature (Fig. 12.1; Hasanuzzaman and Fujita 2011; Hasanuzzaman et al. 2011, 2012, 2014).

12.3 The Role of Selenium in Salt Stress Tolerance

It is estimated that, on a global scale, no other toxic substance has such a considerable limiting effect on plant growth and yield as excessive salinity (Aslam et al. 2011). The wish to obtain high yields quickly by application of intensive fertilisation, in particular in covered cultivation systems, results in soil over-fertilisation inducing salt stress in plants. Additionally, the recent progressive increase in global temperature accompanied by reduced precipitation rates leads to an increase in the area of excessively saline soils. A majority of crop plant species are sensitive even to relatively low salinity of the soil, which leads to lower water availability caused by reduced water potential in the soil solution. An excess of ions, in particular Na^+ and Cl^-, disrupts the cell ionic homeostasis and may induce oxidative stress (Zhu 2003; Kong et al. 2005). It is estimated that soil salinity affects approx. 20% of irrigated land reducing significantly yielding of plants; therefore, much research has been conducted to develop crops with enhanced salt stress tolerance (Negrão et al. 2017). In recent years, exogenous phytoprotectants such as osmoprotectants, phytohormones, polyamines, antioxidants, and various trace elements have been found useful to mitigate salt-induced damage (Hasanuzzaman et al. 2011). One of these protectants, which displays the capability to improve the growth and stress tolerance of plants to excessive salinity, is Se.

A beneficial effect of Se on plants growing under excessive salinity conditions was noted for different plant species, e.g. sorrel (Kong et al. 2005), cucumber (Hawrylak-Nowak 2009), rapeseed (Hasanuzzaman et al. 2011), melon (KeLing et al. 2013), canola (Hashem et al. 2013), lettuce (Hawrylak-Nowak 2015), tomato (Diao et al. 2014; Mozafariyan et al. 2016), and maize (Jiang et al. 2017). However, the mechanism of Se-mediated salt tolerance has not been fully clarified. Induction of antioxidant machinery by Se in plants grown under salt stress has been reported in a majority of studies, but according to some other studies, this is not the entire effect of this element on the metabolism of salt-exposed plants.

The first studies on the effect of Se application on plant salt stress tolerance were performed by Kong et al. (2005). They demonstrated that, at low concentrations (1–5 μM), Se (applied as selenite) stimulated the growth of NaCl-exposed sorrel. Exogenous Se caused an increase in the activities of superoxide dismutase (SOD) and peroxidase (POX), enhanced the accumulation of water-soluble sugars, and modified cellular ultrastructure. In this study, the biomass of sorrel growing at 100 mM NaCl and treated with 5 μM Se was double that of the plants exposed to 100 mM NaCl alone. Furthermore, Se positively influenced the integrity of cellular membranes and organelles, such as chloroplasts and mitochondria. In chloroplasts, grana dilation was decreased, the thylakoids were more regularly arranged, and the mitochondrial cristae in leaf mesophyll cells became more legible and more numerous due to the Se addition. In addition, the interaction between organelles was more intimate after addition of 5 μM Se than at 100 mM NaCl alone (Kong et al. 2005). Further studies of Jiang et al. (2017) also indicated that Se-selenite application (1 μM Se) alleviated structural damage to chloroplasts induced by NaCl exposition, resulting in a more integrated internal lamella, thicker grana lamellae, and a more regular shape of the thylakoids in the leaf cells than in the plants treated with NaCl alone.

The studies performed by Hawrylak-Nowak (2009) on cucumber grown under hydroponic conditions have confirmed the positive impact of Se on plants growing under salt stress. It was shown that the presence of Se (applied as selenate) under NaCl-induced osmotic stress had a growth-promoting effect mainly on the root system, whose biomass was almost double than in plants exposed to 50 mM NaCl only. The beneficial effect of Se was associated with reduction of the harmful process of lipid peroxidation and an increase in accumulation of photosynthetic pigments. The enrichment of plants with Se inhibited the NaCl-induced increase in lipid peroxidation more clearly in the root cells than in the leaf cells. The Se-induced increase in the stability of the cell membranes under excessive salinity was accompanied by an elevated level of photosynthetic pigments. This may indicate Se-stimulated maintenance of chloroplast membrane integrity under adverse environmental conditions. A detailed insight in the chloroplast antioxidant status in Se-biofortified plants grown under salt exposure was provided by Diao et al. (2014). They found that Se-selenite alleviated NaCl-induced oxidative stress in tomato through regulating the antioxidant defence systems in the chloroplasts, which was associated with the enhancement of the photochemical efficiency of PSII. They found that efficient scavenging of ROS in chloroplasts took place mainly through the ascorbate-glutathione cycle, thioredoxin (Trx), and glutaredoxin (Grx) systems, which might be important mechanisms for Se-mediated scavenging of H_2O_2 and maintenance of a higher reducing power to reduce oxidative damage under salt stress. Such a role of Se in chloroplast metabolism of salt-stressed plants might be associated with further improvement in the photochemical efficiency of PSII, thereby maintaining high photosynthetic rates under stress. Therefore, the restoration of the photosynthetic capacity in salt-treated plants caused by exogenous application of Se observed by Diao et al. (2014) and Jiang et al. (2017) may be related to the increases in chlorophyll content and the preservation of chloroplast ultrastructure by maintaining their proper antioxidant status.

The common antagonism between the Na^+ and K^+ ions is regarded as one of the causes of disturbances in ion homeostasis in plants growing under NaCl exposure. Under salt stress conditions, the maintenance of K^+ and Na^+ homeostasis in cells becomes crucial for plant survival. Plants try to preserve a high level of K^+ and a low level of Na^+ in the cytosol by regulating the expression and activity of Na^+ and K^+ transporters and H^+ pumps that generate the driving force for ion transport (Zhu 2003). In the experiments of Kong et al. (2005) and Hawrylak-Nowak (2009), the Se addition in general neither blocked the uptake of Na^+ nor increased the uptake of K^+. Application of Se to the salinity-affected substrate did not limit the decline in the content of K^+ in the shoots, and the K^+/Na^+ ratio was at a similar level in plants treated with NaCl alone and those further enriched with Se (Hawrylak-Nowak 2009). Although reduced Cl^- content was found in NaCl-exposed cucumber plants supplemented with Se (Hawrylak-Nowak 2009), further studies with lettuce did not confirm this phenomenon (Hawrylak-Nowak 2015). In contrast, Jiang et al. (2017) reported that a low Se concentration (1 μM Se applied as selenite) increased the K^+ content in the shoots but decreased the Na^+ level in the roots of salt-exposed maize. They suggest that in the root cells, Se upregulates the *ZmNHX1* gene expression level, which may be involved in Na^+ compartmentalisation under excessive salinity.

Free proline accumulation is one of the frequent plant responses to osmotic stress caused by drought or excessive salinity. It is believed that proline molecules can act as low-molecular-weight chaperones (Kishor et al. 2005; Gupta et al. 2013). Some researchers did not find any considerable increase in the level of free proline, while others consider elevated proline accumulation merely as a stress effect, rather than a reason of stress tolerance (Kumar et al. 2003). In experiments of Hawrylak-Nowak (2009), cucumber plants exposed to 50 mM NaCl did not accumulate substantially greater amounts of free proline than the control plants. In turn, enrichment of the NaCl-containing substrate with Se increased the concentration of this amino acid in the leaves, compared to plants treated with NaCl only. In the work of Hashem et al.

(2013), foliar spray of salt-stressed canola plants with different concentrations of Se caused a significant increase in proline content compared to the Se-untreated control. However, in this species, also the single salt treatment induced accumulation of free proline. The phenomenon of the Se-induced increase in free proline content combined with the stimulation of plant growth, increased levels of photosynthetic pigments, and reduced lipid peroxidation may indirectly indicate a beneficial role of free proline in salinity tolerance. On the other hand, the reasons and mechanisms for increased proline accumulation in Se-supplied plants exposed to salt stress have not been studied. In turn, in the study of Hawrylak-Nowak (2015) on lettuce, an increase in the proline level after NaCl exposition was found, but the level of free proline in salt-stressed plants supplemented with Se (applied as both selenite and selenate) did not differ from that in plants treated with NaCl alone.

Under salt stress conditions, enrichment of tomato plants with Se increased their biomass, maintained tissue hydration, and contributed to improved cell membrane stability. There was also a significant impact of Se on enzymatic reactions catalysed by catalase (CAT), whose activity was significantly reduced by salinity, but after the application of Se, it retained values similar to those noted in the control plants. No similar correlations were noted in the case of POX (Mozafariyan et al. 2016). However, KeLing et al. (2013) noted an increase in SOD and POX activities in melon plants subjected to salt stress, while CAT activity was generally not enhanced. It also seems that the Se-induced increase in tomato tolerance to the elevated levels of NaCl in the substrate was not associated with changes in the endogenous content of phenolic compounds and proline (Mozafariyan et al. 2016).

Another aspect of the role of Se in plant salt tolerance was examined by Hasanuzzaman et al. (2011). They analysed the involvement of the methylglyoxal (MG) detoxification system in Se-induced resistance of rapeseed seedlings to salt exposition. Methylglyoxal is a highly reactive cytotoxic compound produced intracellularly through different enzymatic and non-enzymatic reactions. In plants, MG can be detected under optimal growth conditions, but its accumulation increases under environmental stresses. In plant cells, it is neutralised largely by the glyoxalase system, which includes two enzymes, glyoxalase I (Gly I) and glyoxalase II (Gly II). Overexpression of the glyoxalase enzymes has been found to limit oxidative stress and MG accumulation under stress conditions by maintaining reduced glutathione (GSH) homeostasis and antioxidant enzyme activities (Yadav et al. 2008). Hasanuzzaman et al. (2011) revealed that exogenously applied Se-selenate in salt-exposed rapeseed caused an increase in the ascorbate (L-AA) and GSH contents, elevated the GSH/GSSG ratio, and enhanced the activity of antioxidant enzymes as well as stimulated the glyoxalase system machinery. As a result, a decrease in H_2O_2 accumulation and reduced lipid peroxidation was found in Se-biofortified plants exposed to NaCl, compared to salt stress alone. They concluded that the antioxidant machinery and glyoxalase cycle were upregulated in the presence of Se and the control of the levels of ROS and MG during stress was more efficient in maintenance of redox homeostasis in the cells.

The chemical form of Se used for biofortification may also have considerable importance for the expected increase in plant tolerance to stress. Hawrylak-Nowak

(2015) found that, from two investigated inorganic Se forms, selenite was more effective in alleviation of salt stress in lettuce than selenate. Selenium was applied at the concentrations of 2 or 6 μM to the nutrient solution containing 40 mM NaCl. It was demonstrated that the application of Se in the form of selenite into the salinity-affected medium stimulated the growth of the root system, whose biomass was by 37–69% higher than in plants growing in the presence of 40 mM NaCl alone. The biomass of the aboveground parts also increased as a result of the selenite addition but only after the application of 2 μM of this selenium form. On the other hand, enrichment of the salt-stressed plants with selenate did not cause such distinct positive effects as in the case of selenite. In the presence of 2 μM selenate, an increase in root system biomass only was noted. In turn, the increase in the selenate concentration to 6 μM did not stimulate the growth of NaCl-exposed lettuce. These results suggest that the beneficial effect of Se on lettuce grown under salt stress conditions is dependent on the chemical form of Se and is primarily associated with stimulation of the root system growth. Moreover, unlike in the case of cucumber (Hawrylak-Nowak 2009), lettuce (Hawrylak-Nowak 2015) exposed to NaCl did not exhibit reduced Cl^- accumulation in the aboveground parts or significant fluctuations in the proline level as an effect of Se supplementation.

The results of Hashem et al. (2013) revealed that foliar application of Se improved canola oil quality under salt stress. An increase in oleic, linoleic, and linolenic acid contents in oil from seeds produced by Se-treated plants was noticed. Linoleic and linolenic acid are among the most important components of oil, because they are dietary essential fatty acids and cannot be produced by humans. Furthermore, Se application caused reduction in erucic acid content in canola oil, which makes it more appropriate for the market standards and safer for human consumption.

12.4 Selenium Improves Drought Tolerance of Crop Plants

Drought is considered the most destructive environmental stress, which decreases productivity of crops more than any other abiotic stress, and the most critical threat to world food security. The severity and duration of drought is unpredictable as it depends on numerous factors such as occurrence and distribution of precipitation, evaporative demands, and soil water storage capacity (Farooq et al. 2009).

One of the first studies on the role of Se in water deficit tolerance by plants was that carried out by Kuznetsov et al. (2003) on spring wheat. They found that Se increased the resistance of plants to drought by regulating their water status. Under drought conditions, the exogenous application of Se in the form of selenite to the soil caused an increase in the water uptake capacity by the root system, rather than by a more economical use of water in the transpiration. In this experiment, the Se supply did not inhibit transpiration but caused even a slight increase in the rate of this process. Moreover, the Se supplementation provoked inhibition of drought-induced accumulation of free proline and a decrease in POX activity, which the authors imply as indirect evidence for the antioxidant role of Se. Similar results were obtained by Proietti et al. (2013), who found that foliar application of Se (but in the form of selenate) under drought stress increased the photosynthesis rate and fruit yield in olive through regulation of the tree water status by maintaining an adequately high level of water in the leaves. They also found that the correct water balance was not achieved by the inhibition of the transpiration rate, which instead was elevated than in the Se-untreated and drought-stressed trees, but probably by stimulation of water uptake by roots. In addition, the Se application induced an increase in the activity of some antioxidant enzymes (ascorbate peroxidase (APX), CAT, and GPX) and inhibited lipid peroxidation. Therefore, it was concluded that Se ions were able to improve plant drought tolerance through modulation of plant antioxidant machinery. Almost all studies with Se-enriched plants growing under drought stress reported induction of antioxidant enzyme activity and/or an increase in the non-enzymatic antioxidant level, which reduced the concentration of some prooxidative compounds (Kuznetsov et al. 2003; Sajedi et al. 2011; Ibrahim 2014; Proietti et al. 2013; Nawaz et al. 2013, 2015, 2016). For example, in Se-pretreated wheat plants subjected to drought, the accumulation of H_2O_2 and the level of lipid peroxidation were decreased, whereas the activities of the antioxidant enzymes (CAT, SOD) and the content of the non-enzymatic antioxidants (L-AA, GSH) were increased. In consequence, the membrane stability index and root viability of the Se-pretreated plants were elevated under stress conditions. On the other hand, the activities of POX as well as the content of proline and α-tocopherol were reduced in the Se-pretreated and drought-stressed plants, which may indicate mitigation of oxidative stress by the Se pretreatment (Ibrahim 2014).

Nawaz et al. (2013) tested the efficiency of seed priming in Se-selenate solutions (25–110 μM) as a method for improving seed performance and increase tolerance of wheat to drought. They found that, although the plant biomass was not affected by seed priming with Se under optimal water conditions, it increased with the increase in the Se concentration under drought. The optimal condition for enhancing drought tolerance in wheat seedlings was seed priming in a 75 μM Se solution for 1 h. Similarly, Yao et al. (2009) searched the optimal concentration of Se supply that will be favourable for growth of wheat during water deficit. It was shown that the highest (3.0 mg Se kg^{-1}) and lowest (0.5 mg Se kg^{-1}) amount of Se-selenite in the soil did not affect the biomass of plants, whereas treatments with 1.0 and 2.0 mg Se kg^{-1} promoted growth of wheat under water stress. Moreover, in the presence of 1.0, 2.0, and 3.0 mg Se kg^{-1}, the root activity, content of free proline, POX and CAT activities, and photosynthetic pigment content were increased, while lipid peroxidation was reduced.

In later studies, Nawaz et al. (2015) compared three various methods of Se-selenate application to evaluate their efficiency in alleviation of drought stress consequences in spring wheat. They indicated that the foliar spray with Se was more effective than Se fertigation or Se seed priming. They found a Se-stimulated increase in the concentration of some osmoprotectants (such as total soluble sugars, free proline, and total free amino acids) and recorded enhanced activity of POX, CAT, and APX that ultimately improved the wheat grain yield and quality in conditions of drought. Under water deficit, the grain yield was enhanced by 64% and 52% after

Se fertigation and Se foliar spray, respectively, compared to the Se-untreated control. The Se supply also influenced the accumulation of several nutrients in grains obtained from drought-stressed wheat. The plants grown from Se-primed seeds were characterised with high grain P content; however, a decrease in the P concentration was noted in the grains of plants receiving Se by fertigation and foliar spraying with Se. On the other hand, the Zn, Fe, and Mg concentrations in grains increased after the exogenous Se supply. The authors suggest that the primary effect of Se on nutrient accumulation might be attributed to the Se ion interaction with the transport of other ions across plasma membranes by changing their permeability coefficient to some ions (Nawaz et al. 2015).

More recently, Nawaz et al. (2016) found an increase in the photosynthetic rate and stomatal conductance of Se-treated wheat grown under water deficit and suggested that this effect was caused by the positive influence of Se ions on turgor maintenance and stimulation of antioxidant machinery. Consequently, foliar spray with a Se-selenate solution improved the yield and fodder quality attributes, e.g. crude protein, fibre, and Se contents. Similarly, Tadina et al. (2007) found that two cultivars of the common buckwheat treated with foliar spray of a Se-selenate solution that were exposed to water deficit had higher stomatal conductance. Additionally, a significantly higher actual photochemical efficiency of PSII was noted in one of the cultivars treated with Se under drought stress, while the potential photochemical efficiency of PSII was not enhanced. However, the yield was significantly highest in plants exposed to Se alone.

In a field experiment, Sajedi et al. (2011) found that the antioxidant activity in drought-stressed maize supplied with Se-selenite was enhanced and the corn grain yield increased, particularly at the highest level of drought. They indicated that Se fertilisation at the grain filling stage resulted in the highest grain yield under water deficit. On the other hand, the simultaneous use of Se and micronutrient fertilisation negatively affected the antioxidant status and grain yield suggesting the occurrence of antagonism between Se and micronutrients and their combined use is not recommendable in conditions of drought (Sajedi et al. 2011). Studies conducted by Emam et al. (2014) under field conditions indicated that Se-selenate pretreatment alleviated the adverse effects of drought and improved the yielding of rice at the full maturity stage. Selenium pre-soaking (0.03 mM Se) stimulated an increase in cellulose, lignin, and pectin contents of rice straw compared with drought-exposed plants but not treated with Se. Additionally, it was demonstrated that pre-soaking of grains in a selenate solution not only resulted in amelioration of the threats caused by drought but also improved yield quality under water deficit by increasing the levels of total soluble carbohydrates, starch, amylose, phenolic compounds, flavonoids, oil, as well as inorganic Ca and P in rice grains.

According to the findings of Kostopoulou et al. (2015), irrigation of yellow sweet clover with a Se-selenate solution before the occurrence of water deficit induced improved accumulation of some inorganic ions in the shoots of this species under drought. An interaction between Se supplementation and water treatment was more considerable for Ca and Mg, whose contents decreased under water deficit at a low Se concentration, and for Zn and Cu, which increased under water stress at a high

Se dose. Similarly, Wang (2011) studied the effect of Se application (5 μM as selenate) on drought tolerance in white clover. The Se-supplemented plants exposed to short-term water deficit (imposed by polyethylene glycol, PEG) had higher biomass, relative water content (RWC), and chlorophyll concentration than the drought-stressed plants. Application of Se also reduced lipid peroxidation and H_2O_2 accumulation. Moreover, the activity of SOD that increased during the water deficit was further promoted by Se supply. In turn, Se application under drought conditions had no effect on CAT activity but increased APX and glutathione reductase (GR) activities. However, under field conditions, Habibi (2013) did not note a significant increase in shoot dry mass and seed yield after foliar application of Se-selenate (30 g Se ha^{-1}) in drought-stressed barley, although the shoot biomass increased in Se-treated and well-watered plants. Notwithstanding, Se-supplemented plants grown under water deficit exhibited better protection from oxidative damage, and this ability was related to higher CAT and GPX activities as well as a lower level of lipid peroxidation and H_2O_2 accumulation. On the other hand, the analysed indicators of PSII photochemistry and gas exchange were not affected by Se supplementation under drought stress.

Germ (2008) observed a marked decrease in the respiratory potential and biomass of Se-treated potato tubers exposed to water deficit, while the Se treatment had no effect on the number and size of leaf stomata. The effects of drought and Se-selenate treatment were however cultivar-specific; thus, the authors suggest that the results from certain cultivars cannot be extrapolated to the whole species. The speciation of Se in tubers obtained from foliar Se-sprayed potato plants grown under optimal or deficit water conditions was the subject of research performed by Cuderman et al. (2008). They found that, in plants treated with Se-selenate, selenate and SeMet were the main soluble Se species (representing 51–68% of total Se) in the potato tubers, regardless of the degree of water supply of plants.

Given the abovementioned information, the protective role of Se under water deficit could be attributed to several mechanisms: (i) regulation of plant water status by enhancement of root water uptake, (ii) protection of cells from oxidative damage, (iii) stimulation to accumulation of compatible solutes, and (iv) regulation of the level of some inorganic ions in plant organs.

12.5 Enhanced Resistance of Se-Biofortified Plants to Thermal Stresses

In plants, temperature stress is classified into three types depending on the stressor, which may be high, chilling, or freezing temperature. Both too low and too high temperatures, in relation to the physiological requirements of the species, are harmful and can damage crop plants and limit their distribution and yield. Haghighi et al. (2014) noted beneficial effects of Se (applied as selenite or nano-Se) on tomato grown under short-term suboptimal or high temperatures. At a low concentration, the Se compounds applied promoted plant growth and increased the relative water content. Se-selenate and nano-Se had similar positive influence on some growth parameters, but not all of them. When applied at 2.5 μM, Se-selenate was more effective than nano-Se, improving shoot and root biomass, shoot diameter, and root volume. However, it should be taken into account that, in general, a higher ambient temperature induces greater uptake of Se by plants (El-Ramady et al. 2016).

The effect of Se applied as selenate (2.5–20 μM) on the resistance of cucumber, a plant species sensitive to low-temperature stress, was investigated by Hawrylak-Nowak et al. (2010). Plants growing initially at optimum temperature were treated with a short-term cold stress: 10/5 °C (day/night, 24 h) followed by 20/15 °C (day/night, 24 h). After the low-temperature treatment, the plants grew for the next week at optimum temperature. It was shown in this experiment that plants growing in the presence of Se were characterised by a higher level of free proline relative to the control, both immediately after the cold stress and after the next 7 days of growth at optimum temperature. However, the level of this amino acid was substantially higher immediately after the stress. The positive correlation between the accumulation of free endogenous proline and the higher cold resistance in plants was confirmed primarily in species that are resistant to low temperature (Kishor et al. 2005; Kaur et al. 2011). In turn, in a majority of plants that are sensitive to cold, free proline accumulation does not induce an increase in their tolerance to this stress factor, unless proline is exogenously applied prior to stress. The most probable roles of proline are to (i) regulate cytosol acidity, (ii) stabilise the NAD^+/NADH proportion, (iii) maintain the photochemical activity of PSII, and (iv) protect against lipid peroxidation (Theocharis et al. 2012). Therefore, the Se-induced increase in the proline level observed in the study of Hawrylak-Nowak et al. (2010) may potentially contribute to increased tolerance of cucumber to cold stress. This mechanism can be confirmed by the reduced lipid peroxidation in the roots of Se-biofortified plants, in comparison to plants that are not enriched with this element. On the other hand, although the application of Se modified the physiological response of cucumber to cold stress by increasing the level of proline in leaf tissues and inhibiting lipid peroxidation in root tissues, the resistance of this species to low temperature was not distinctly higher, since the biomass of the Se-biofortified plants and the level of photosynthetic pigments were not significantly different in comparison with plants that were not biofortified with Se. However, Chu et al. (2010) demonstrated in a pot experiment that Se-selenite supply could increase both the growth and antioxidant capacity of wheat seedlings. In their study, the optimal Se fertilisation (1.0 mg Se kg^{-1} of soil) reduced production of ROS and decreased lipid peroxidation. Additionally, the content of antioxidant compounds (anthocyanins, flavonoids, and phenolic compounds) as well as the activities of antioxidant enzymes (POX, CAT) increased after application of different Se concentrations under cold stress.

Oxidative stress is commonly induced when plants are grown under thermal stress. Decreased antioxidant defence under heat resulting in lower sorghum grain yield was noted by Djanaguiraman et al. (2010). Foliar application of Se (75 mg L^{-1} as selenate) a few days before heat stress caused a decrease in membrane injury by enhancing antioxidant defence, thereby resulting in higher grain yield. The increase in antioxidant enzyme activities (CAT, POX) and decrease in ROS accumulation induced by Se were greater in plants grown under high-temperature stress than in those grown under optimal temperature. Hasanuzzaman et al. (2014) formulated similar conclusions in experiments with rapeseed, where Se-assisted upregulation of antioxidant defence was noted only under high-temperature stress. In this study, many antioxidant enzymes, such as monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), GR, GPX, CAT, Gly I, and Gly II, showed enhanced activities in Se-supplemented and heat-treated rapeseed plants. In recent studies, Iqbal et al. (2015) demonstrated that foliar application of Se-selenate reduced oxidative stress and enhanced grain yield of wheat under high-temperature stress. Both enzymatic (CAT and APX activities) and non-enzymatic (anthocyanins, carotenoids, and L-AA contents) antioxidants were elevated, while oxidants (H_2O_2, lipid peroxidation products) decreased after Se application under heat stress conditions. Moreover, the authors suggest that Se-assisted upregulation of antioxidative defence helped the studied wheat cultivars (drought tolerant and drought sensitive) to increase fertility and thereby avoid decrease of grain yield under high temperature. Foliar application of a Se-selenate solution (8 μM) at the flower initiation stage also reversed heat-induced oxidative damage by strengthening antioxidative protection in cucumber (Balal et al. 2016). In this study, Se supplementation enhanced the antioxidative enzyme activities (SOD, POD, CAT, APX, GPX, and GR) and caused reduction in ROS and lipid peroxidation levels. A marked elevation in the activity of enzymatic antioxidants and a decrease in ROS accumulation were noted also in roots of Se-sprayed plants, indicating that Se from foliar application was translocated to the root system and improved the antioxidative mechanism. Moreover, as in the experiments of Djanaguiraman et al. (2010) and Hasanuzzaman et al. (2014), the induction of antioxidative enzyme activities after Se application was greater in heat-exposed plants than in those grown under optimal temperature.

The reduced form of glutathione (GSH), ascorbate (L-AA), and free proline can serve as non-enzymatic antioxidants in prevention and limitation of cell damage under oxidative stress. The ascorbate-glutathione cycle is important in maintenance of cellular homeostasis and plays an important role in removal of excessive amounts of ROS (Dresler and Maksymiec 2013). In a study of Hasanuzzaman et al. (2014), the content of free proline, L-AA, and GSH as well as the GSH/GSSG ratio was enhanced in heat-treated rapeseed plants supplemented with Se-selenate. This modulation/activation of antioxidant machinery protected the seedlings from lipid peroxidation and over-accumulation of H_2O_2. Similarly, Chen and Sung (2001) reported that priming of bitter gourd seeds with a Se-selenite solution partially protected them against suboptimal temperature. The priming-enhanced seed germination was related to the free radical scavenging activities linked to the ascorbate-glutathione cycle. Nevertheless, GPX was the only enzyme that displayed positive response to increasing Se concentrations, suggesting indirectly that this enzyme is Se inducible.

Photosynthesis is one of those most temperature-stress-sensitive physiological processes in plants. In the photosynthetic machinery, the major targets of heat stress are photosynthetic pigments, thylakoid membranes, PS II, and carbon fixation reactions. It has been established that plant genotypes that are able to maintain photosynthesis under high-temperature conditions often demonstrate greater resistance to high temperature (Jajoo and Allakhverdiev 2017). Balal et al. (2016) demonstrated that foliar application of Se-selenate improved stress-impaired chlorophyll fluorescence attributes, photosynthetic activity, and total chlorophyll content in cucumber plants subjected to high temperature. On the other hand, Se supplementation did not influence the intercellular CO_2 concentration under optimal temperature but caused reduction of this parameter under heat stress. The authors suggest that the Se-induced improvement in the photosynthesis rate, growth, and productivity of cucumber under heat stress was associated with enhanced antioxidant activities and increased accumulation of selected osmolytes (proline, glycinebetaine, and total soluble sugars). Moreover, they found that the application of Se caused an increase in stomatal conductance and the transpiration rate both under stress and normal temperature conditions.

12.6 Role of Selenium in Trace Metal Stress Tolerance

Trace metal toxicity is becoming one of the major abiotic stresses for plants as the amounts of toxic metals in the environment have been increasing considerably in many regions of the world due to both natural processes and urbanisation and industrialisation. Metal contamination in cultivated soils can originate from atmospheric pollution, use of pesticides and chemical fertilisers, and irrigation with poor-quality wastewater. Although some metals are essential at physiological concentrations (macro- and micronutrients), they can be harmful for plants in excess (Hasanuzzaman and Fujita 2012; Masarovičová and Kráľová 2012). Many studies have reported a positive role of low Se concentrations in protecting plants from trace metal toxicity. It can be attributed mainly to the Se-mediated mitigation of metal-induced oxidative stress and, as a result of lower uptake of metals by plants, modification of their translocation, decreasing metal mobility in soils, as well as alteration of cell membrane structure (Hu et al. 2014; Sieprawska et al. 2015; Gupta and Gupta 2017).

Photosynthesis disturbances that are often observed at trace metal excess were considered as the main cause of increased ROS accumulation and induction of oxidative stress (Sieprawska et al. 2015). Selenium used at low concentrations can reduce excess ROS generation and enhance the antioxidant system, thereby improving plant defence against subsequent oxidative damage. Such a Se-induced effect has been shown in many studies. Cartes et al. (2010) found Se-selenite mitigated Al-induced toxicity in roots of ryegrass mainly by increasing spontaneous dismutation of $O_2^{\bullet-}$ to H_2O_2 and subsequent activation of the POX enzyme. In the study of Filek et al. (2008) on rape seedlings, the addition of Se-selenate to a Cd-containing medium overturned the Cd-induced increase in H_2O_2 accumulation and decreased the level of lipid peroxidation. However, Se applied separately or in combination with Cd did not affect the activity of antioxidative enzymes in the roots but diminished their activity in the leaves. Mroczek-Zdyrska et al. (2017) showed that a low concentration of Se-selenite (1.5 or 6 μM) alleviated the toxicity of Pb in faba bean plants grown under phosphorus-deficient conditions (the addition of phosphate to a Pb-containing growth medium reduces the phytoavailability of Pb). The beneficial, mainly antioxidative, impact of Se was manifested by decreased H_2O_2 and $O_2^{\bullet -}$ accumulation and modified activity of GPX, POX, and CAT. In similar studies on the effect of Se-selenite on As-arsenite toxicity in rice (Chauhan et al. 2017), an increase in the concentration of antioxidative phenolic compounds was found, particularly gallic acid, ferulic acid, protocatechuic acid, and rutin. Moreover, the application of Se increased thiol metabolism-related enzymes, e.g. serine acetyl transferase (SAT) and cysteine synthase (CS). Most likely, because of the antioxidative functions of Se, an increase in photosynthetic efficiency in the presence of Se ions was detected in plants growing under excess of some trace metals (Łabanowska et al. 2010; Filek et al. 2010b). Based on measurements of some photosynthesis indicators, it was suggested that Se might stimulate of energy flux through the transport systems in PS II (Sieprawska et al. 2015).

The relevant mechanism of trace metal detoxification induced by Se may be connected with the inhibition of uptake and translocation thereof from roots to shoots. The presence of Se-selenite in the Cd-containing medium significantly limited the translocation of this metal to the generative organs of pepper and had a positive effect on selected generative parameters (number of flowers, number and diameter of fruits), consequently, increasing the yield of the Cd-exposed pepper (Mozafariyan et al. 2014). Similarly, Hu et al. (2014) demonstrated that Se-selenite application markedly decreased the concentrations of Cd in rice grains, but Se biofortification had no significant effect on grain Pb accumulation. Furthermore, they found that the Se application significantly decreased metal mobility and bioavailability in soils and inhibited the translocation of these metals from the soil to an iron plaque. A similar limiting effect of Se-selenite on Cd uptake by rice was found by Lin et al. (2012).

In a recent study of Wu et al. (2016), exogenously applied Se-selenite markedly reduced the concentration of Cd and Pb in both roots and aboveground organs of oilseed rape and inhibited the root-shoot translocation of these metals. Hawrylak-Nowak et al. (2014) found that application of Se-selenate to a Cd-containing nutrient solution reduced the Cd concentration in the roots but only in plants exposed to the higher concentrations of Cd (50 μM). Nonetheless, such reduction was not observed either in the aboveground parts or in the 25 μM Cd-exposed plants. Therefore, the authors imply that the influence of Se on accumulation of Cd was organ- and dose-dependent. Meanwhile, in a pot experiment with cucumber, Sun et al. (2016b) found selenite-stimulated reduction of the Cd concentration in leaves, stems, and roots. Additionally, Se applied as SeO_2 inhibited the accumulation of all metals tested (Cd, Cu, Pb, Zn) in mustard shoots, and the strongest inhibition was observed for phytoaccumulation of Pb (Fargašová et al. 2006). A similar pattern of Se action on Cd distribution was observed by Pedrero et al. (2008) in broccoli. When Se-selenite was added simultaneously with Cd, the accumulation of this metal in the roots was higher than when Cd was applied alone. However, this enhanced accumulation of Cd in roots coincided with reduced Cd content in leaves and fruits, suggesting that the translocation of Cd in the presence of Se was limited. This phenomenon may indicate that Se generates some barriers to metal transfer from the roots to the aboveground organs. In studies of Shanker et al. (1996), the application of Se (in the form of selenite or selenate) to the Cd-contaminated soil caused reduction in the content of this metal in maize, but the decline in the Cd accumulation was greater in the roots than in the shoots. On the other hand, no significant differences in the uptake of this metal were observed for the two chemical forms of Se tested in this study. Conversely, the application of Se-selenite did not alter the Pb accumulation in the roots (Mroczek-Zdyrska and Wójcik 2012) and shoots (Mroczek-Zdyrska et al. 2017) of field bean grown in a Pb-containing nutrient solution.

It is worth emphasising that, in some cases, Se supply can stimulate the phytoaccumulation of trace metals, such as Cd and Cu in mustard (Fargašová et al. 2006), As in *Thunbergia alata* (Bluemlein et al. 2009), or Cu and Cd in wheat and pea (Landberg and Greger 1994). For instance, Se-selenite application caused an increase in Cd concentrations of pea roots up to 300%, and Se-selenate elevated the Cd level in wheat shoots up to 50% (Landberg and Greger 1994).

Investigations of Hawrylak-Nowak et al. (2014) on the effect of Se-selenate on Cd toxicity in cucumber showed that the mutual proportion between the concentrations of these elements in the rhizosphere was crucial for the response of this species to Cd toxicity. Among the Se concentrations used, only the application of 10 μM Se to the medium containing 50 μM Cd had a positive effect on the root system growth and some physiological parameters of the plants. A similar conclusion was reached by Balakhnina and Nadezhkina (2017), who found that the effectiveness of Se-selenate application on the adaptive potential of plants cultivated on soils contaminated with Pb strongly depended on the mutual concentrations of Se and Pb ions. Additionally, Hawrylak-Nowak et al. (2014) demonstrated that the presence of Se in a Cd-containing medium decreased the accumulation of phytochelatins (PCs) in cucumber roots. The Se-induced decrease in the PC level may have been caused by substitution of S with Se in the functional cysteine (Cys) groups and substitution of Cys with SeCys, e.g. in the catalytic centre of phytochelatin synthase, which, in consequence, may have caused inhibition of the PCs synthesis. The advantageous effect of Se on the growth of Cd-treated cucumbers was limited exclusively to their root system and was probably associated with limitation of Cd accumulation in root tissues, inhibition of the harmful lipid peroxidation in these organs, and an increase in the stability of cell membranes in leaf cells (Hawrylak-Nowak et al. 2014). On the other hand, Bian et al. (2016) demonstrated a negative synergistic interaction between Se and Hg ions. In Hg-exposed Chinese cabbage, the supplementation of plants with Se-selenite caused inhibition of root growth, enhanced ROS accumulation, and increased lipid peroxidation. It also modified the activity of antioxidant enzymes and led to loss of plasma membrane integrity in roots relative to individual treatments with these elements.

It has been suggested that the regulation of uptake and distribution of essential elements by Se ions can be a significant mechanism preventing unfavourable changes in the mineral status of plants exposed to metal excess. Interactions between Se and S ions have been extensively studied due to the chemical similarity of these elements and the use of the same metabolic pathway (El-Ramady et al. 2016). Zembala et al. (2010) found that Se-selenate in Cd-stressed rape and wheat plants tended to counterbalance Cd-induced changes in some essential nutrient concentrations. Quantitatively, the preventing effect of Se was more evident for micronutrients than for macronutrients. For example, in rape roots, the Cd-induced 70% drop in the B concentration levelled off in the additional presence of Se. Moreover, the Fe content in the roots of rape and wheat increased significantly when the Cd-treated plants were supplemented with Se. Referring to this, Feng et al. (2013) hypothesised that the regulation of the Fe level in Se-biofortified plants may represent important mechanism of alleviation of adverse effects of abiotic stresses. The most recent study of Chauhan et al. (2017) on rice also showed that, besides amelioration of As-induced toxicity by reducing As accumulation, Se-selenite caused restoration of As-impaired micronutrient balance. The application of Se repaired the nutrient deficiency during As stress by increasing the level of Fe, Mn, Cu, Co, Mo, and Zn in both roots and shoots. Analogously to the experiments of Zembala et al. (2010), a considerable increase in the Fe level was noted in the roots of this species. In turn, the supplementation of Cd-treated rice plants with Se-selenite showed a tendency to counterbalance Cd-induced decreases in leaf Mn and Zn concentrations and increases in root Zn as well as leaf and root Cu contents (Lin et al. 2012). However, since there is limited research in this area, the information about the effect of Se ions on the uptake and translocation of macro- and micronutrients in metal-stressed plants is still insufficient.

Cell membranes are among the first targets of a number of abiotic stressors, and the maintenance of membrane stability and integrity is of crucial importance for stress tolerance. Moreover, the cell membrane plays a fundamental role in the homeostasis of toxic metals, preventing or reducing their entry into the cell. Interesting information in this respect was provided in research performed on isolated wheat chloroplast/plastids (Filek et al. 2009, 2010a). The in vitro study on wheat (Filek et al. 2009) showed that the application of Se-selenate under Cd stress caused some decrease in the amount of accumulated Cd and induced partial remodelling of the membrane lipid composition disturbed by this metal by an increase in lipid fatty acid unsaturation. However, the Se supply did not prevent Cd-induced changes of other investigated membrane properties and did not reduce the blocking effect of Cd on embryogenesis. In further studies on rape plants (Filek et al. 2010a), it was found that Se-selenate partly counterbalanced the destructive effects of Cd leading to an increase in the chloroplast size and rebuilding the chloroplast ultrastructure. The lipid and fatty acid composition of chloroplast envelopes altered by Cd ions exhibited a decrease in the digalactosyldiacylglycerol content and an increase in the content of monogalactosyldiacylglycerol and phospholipid fractions, as well as an enhancement of the fatty acid saturation of all lipids studied. The changes in the fatty acid saturation correlated well with the decrease in membrane fluidity. The presence of Se ions in the Cd-containing medium partially reversed the detected changes, especially fatty acid saturation and membrane fluidity.

An additional possibility of Se action on the biomembrane structure and function has also been demonstrated. This element can exert a direct influence on the activity of membrane protein transporters. It is believed that inhibition of photosynthesis by excess of trace metals is related to chloroplast protein impairment by irreversible binding of metal ions to the SH groups of enzymes and membrane proteins. Hence, Se ions can avoid such binding through 'inactivation' of metals even before their binding to proteins (in the form of $MeSeO_{3(4)}$) and/or by formation of SeH groups in proteins (because of the chemical similarity of Se and S). This gives other possibilities for the formation of bonds in protein transporters (Sieprawska et al. 2015). The impact of Se-selenate on trace metal modification of ion channel activities was indicated by Dziubinska et al. (2010). They noticed a negative impact both of Cd and Se ions on conductance of slow vacuolar channels in rape vacuoles. There was no additive effect of both ions acting together, which suggests that they influenced the same 'inhibitory' mechanism.

In human and animal cells, Se is believed to exhibit strong ability to interact with some trace metals (Hg, Ag, Cd, Tl) to form nontoxic Se-metal complexes. However, such nontoxic Se-metal complexes have not yet been identified in plants (Feng et al. 2013). Yathavakilla and Caruso (2007) studied the interactions between Se-selenite and Hg ions in greenhouse-cultivated soybean treated with these elements and then analysed their metabolised species in different plant organs. They found that most of the water-soluble Hg was localised in the root cells in association with Se in a high molecular weight entity. The Se distribution pattern in plants was unaffected by Hg ions, but the content of Se was found to be higher in plants treated with Hg. Similarly, Bluemlein et al. (2009) did not find As complexes containing Se peptides or mixed As-Se peptides in *Thunbergia alata* exposed to Se-selenite and As-arsenite.

Recent molecular studies have provided valuable information about the protein profile and the possible role of other molecular mechanisms associated with Se-induced resistance to trace metal excess (Pandey et al. 2015; Sun et al. 2016a). The investigations of Pandey et al. (2015) suggest that some role in the antagonistic effect of Se on As-stressed rice seedlings may be played by miRNAs, i.e. small non-coding RNAs. They suggest a possible role of miR395 and miR398 in the ameliorative influence of Se on As phytotoxicity. In turn, through comparative proteomic analyses, Sun et al. (2016a) revealed that there were several complex metabolic interactions leading to Se-improved tolerance to Cd toxicity in cucumber. They demonstrated that the differential relative abundance of metabolism-associated proteins involved in the glycolysis and nitrate assimilation pathways increased Cd tolerance after Se-selenite addition. The higher abundance of photosynthesis-related proteins induced by Se may be involved in mediating electron transfer and/or affect the protein biosynthesis in the chloroplast, thus regulating the photosynthesis rate. Additionally, several proteins involved in amino acid biosynthesis and storage, which may play important role in Se-assisted tolerance to Cd, were detected. It was shown that 21 (10 in leaves and 11 in roots) of the 26 identified Cd-influenced proteins exhibited higher amounts in Se-treated plants, including glutathione *S*-transferase F8, heat shock protein STI-like, peroxidase, ascorbate oxidase, fructose-bisphosphate aldolase 2, NiR, Rieske-type iron-sulphur subunit, and PsbP domain-containing protein 6. Moreover, the presence of Se ions in a Cd-contaminated medium prevented changes in the DNA methylation pattern triggered by toxic Cd concentrations in rape seedlings (Filek et al. 2008) and increased H^+- and Ca^{2+}-ATPase activities in rice (Lin et al. 2012).

12.7 Impact of Selenium on Plants Exposed to UV Radiation

Enhanced UV-B radiation has a profound impact on agricultural production, as UV-B has the highest energy per photon of all the solar wavelengths in the biosphere. In consequence, UV-B photons may directly lead to photomodification of DNA, proteins, and lipids. Therefore, exposure to high UV-B radiation can cause disruptions in metabolism in plants cells and, in turn, can alter the nutritional value, pest and disease tolerance, sexual reproduction, and hardiness of plants (Jansen 2017). It is believed that UV-B hits several targets, particularly on the electron transport side of the PSII reaction centre, resulting in inefficient use of energy (Breznik et al. 2005). However, Shanker (2006) claims that there is a lack of well-designed and replicated experiments in the field due to problems in simulating natural levels of UV-B irradiance under field conditions.

Hartikainen and Xue (1999) were the first to show the positive effect of Se fertilisation on UV-B-exposed plants. In pot experiments with ryegrass and lettuce, they found selenate-stimulated plant growth, but only under enhanced UV-B exposition, which indicates that UV-B irradiance acted as a trigger for the growth-promoting effect of Se. The positive influence of Se under high-energy light exposition was also manifested by increased concentrations of soluble proteins and nucleic acids, inhibited lipid peroxidation, and significant stimulation of GPX activity.

In the relatively well-designed open-field experiments of Heijari et al. (2006), the effects of enhanced UV-B radiation and Se-selenate addition were evidently different in different varieties of strawberry in successive seasons during two experimental years. This may have been related to the practical inability to control differences in precipitation, temperature, and other biotic and abiotic factors under field conditions. In this study, the Se supplementation did not mitigate the harmful effects of UV-B. Although the lower Se dose provoked an increase in leaf growth, the proportion of Se counteracting the impact of UV-B stress was not sufficient to meet the criteria of Se as a mitigating agent.

In another field experiment performed by Yao et al. (2013), the exposition of winter wheat to enhanced UV-B exerted a negative impact on plants, e.g. reduction of growth, lower grain yield and grain protein content, and increased oxidative stress, and influenced the concentration of nutritional elements in wheat grain. Foliar application of Se-selenite at the concentration of 30 mg Se kg^{-1} of the solution at the regreening stage induced a marked increase in total chlorophyll content, spike length, weight per spike, grain yield, grain protein content, and grain N, Fe, Cu, and Se concentration under both ambient and enhanced UV-B levels. These results indicate that Se supply may increase the yield to some extent and improve the quality of grain of winter wheat exposed to enhanced UV-B. In another study, Yao et al. (2014) indicated that the UV-B-induced negative changes in wheat yield and quality were probably the most intense during the heading and flowering stages. Therefore, for better protection of wheat against UV-B damage, selected methods of tolerance enhancement (e.g. Se fertilisation) should be undertaken during the heading and flowering stages. In turn, in their outdoor pot experiment with two buckwheat species, Breznik et al. (2005) demonstrated that the biomass and effective quantum yield of PSII that were reduced by UV-B radiation increased after foliar spray with a Se-selenate solution. The Se treatment under enhanced UV radiation resulted in lower yields of hybrid buckwheat plants although the level of UV-protective substances (e.g. anthocyanins, UV-absorbing compounds) was enhanced under these conditions (Golob et al. 2017b).

Germ et al. (2005) studied the influence of ambient and filtered solar UV-B radiation on photochemical efficiency, respiratory potential, and yield in pumpkins treated with Se. They found that the Se application increased the yield only under ambient radiation conditions. Moreover, compared with plants grown under ambient solar radiation, those grown under UV-B-free radiation showed a 1.7-fold higher activity of the mitochondrial electron transport system (ETS) in Se-untreated plants and a 1.3-fold higher activity in Se-supplied plants. However, no significant effect of excluding UV-B radiation or Se presence on the photochemical efficiency of PSII was detected. More recently, Golob et al. (2017a) showed that foliar spray with a 10 mg L^{-1} Se-selenate solution under ambient UV radiation provoked a trade-off between the plant investment in primary and secondary metabolism in wheat, as the production of UV-absorbing compounds was enhanced, while the photosynthetic pigment level was reduced. However, the Se treatment had little effect on biomass production, regardless of the presence or absence of UV radiation. On the other hand, although the low Se concentrations activated energy resources connected with photochemical quantum yield and mitochondrial respiration, this was insufficient to diminish the negative impact of UV-B radiation on green alga *Zygnema*; in contrast, the interaction of UV-B radiation and Se led to pronounced negative effects on the analysed energy resources (Germ et al. 2009).

12.8 Summary and Conclusions

Environmental stresses can cause over-accumulation of ROS and induction of oxidative stress in plant cells. It seems that the basic mechanisms involved in the beneficial effects of Se (applied both in the selenite and selenite form) on plants grown under abiotic stress conditions are associated with the ability of this element to modulate the antioxidative machinery and, in consequence, increase their tolerance to oxidative stress induced by these factors. However, it seems that this is not the only mechanism, as different additional effects can be observed after exogenous application of Se, which largely depend on the nature of the stress factor. We suggest that the beneficial influence of exogenous Se application on plants exposed to environmental stresses is a multifaceted network, covering several complex physiological, biochemical, and molecular interactions. Moreover, it is worth emphasising that it is quite easy to assess the responses of individual species or a few plant species to Se in a greenhouse or laboratory, when most often one stress factor affects. However, this may not be the case of natural communities, where there may be a high degree of variation in the effects even within one species under field conditions. Therefore, one of the future challenges to recognise Se-plant interactions under environmental stress will be to study the potential essentiality of Se to plants and to unravel the comprehensive picture of its beneficial role in abiotic stress tolerance under natural conditions.

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Chapter 13
Plant Nutrients and Their Roles Under Saline Soil Conditions

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Abstract It is well established that the nutrients of plant play a vital role in all plant processes starting from the emergence, development, productivity, and metabolism reaching to the promotion and protection of plants. These plant nutrients could be in general characterized as macronutrients (e.g., Ca, Mg S, N, K, and P) and micronutrients (i.e., Fe, B, Cu, Mn, Cl, Ni, Mo, Co, and Zn) as well as beneficial elements (e.g., Si, Se, Na, and V). These previous mineral nutrients also could protect crop plants against both abiotic and biotic stresses by enhancing the plant resistance power and regulating the mineral nutritional status. Therefore, any plant nutritional

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problems (like poor soil fertility, imbalance, and deprived delivery of nutrients) definitely will lead to reduce the global production of foods. Thus, it should protect crop production from different stresses through the appropriate agricultural management. Soil salinity was and still one of these plant stresses. A distinguished role of plant nutrients (e.g., N, K, Se, and Si) in ameliorating soil salinity stress has been reported as well as nano-selenium and nano-silica. Several reports have confirmed the great role of these previous plant nutrients under saline soil conditions. Therefore, this review will focus on the role of selenium and silicon in conventional and nanoforms under saline soil conditions. The phytoremediation of these saline soils and the role of plant nutrients will be also highlighted.

Keywords Plant nutrients · Saline soils · Abiotic stresses · Salinity stress · Selenium · Silicon · Nano-selenium · Nano-silica

13.1 Introduction

It is well known that plants need many essential and beneficial nutrients like other living organisms (e.g., humans and animals). These nutrients include carbon, oxygen, hydrogen, nitrogen, potassium, phosphorus, calcium, magnesium, sulfur, iron, copper, boron, molybdenum, manganese, chloride, zinc, cobalt, nickel, selenium, silicon, etc. These nutrients also have great roles in plant metabolism, biochemistry, growth, and development. Some of these previous nutrients (like potassium) play an important role in enzyme activity and cell expansion, stomatal behavior, and osmoregulation. Concerning calcium and magnesium, these nutrients are main cofactors in plants for more than 300 enzymatic reactions (e.g., energy reactions in metabolism and synthesis of protein and nucleic acid). Regarding other nutrients, copper is a constituent of proteins involved in electron transfer and oxygen transport, whereas manganese is the main nutrient for many plant functions such as transporting of electrons during photosynthesis and forming of riboflavin, carotene, and ascorbic acid. The root development and auxin production can be achieved by zinc (Osman 2013; El-Ramady 2014; El-Ramady et al. 2014a, b; Mitra 2015, 2017; Luo et al. 2016; Secco et al. 2017; Zhang et al. 2017c).

In general, plants uptake their nutrients from soil solution and/or by foliar application for the growth, development, and other processes in plants. The bioavailability of these soil nutrients is totally controlled by many factors including soil characterization (e.g., soil pH, salinity, nutrient biogeochemical cycles, and biophysicochemical processes) and environmental and climatic changes. Some elements (like potassium, calcium, iron, copper, and sodium) could enter the agroecosystems through different soil processes and various human activities such as the application of fertilizers. These soil processes include soil salinization and chemical weathering as geochemical processes and biological processes like the decomposition of soil organic matter. Therefore, the bioavailability of nutrients in arid and semiarid soils is related to drought conditions. This drought could be accompanied by increases in soil salinity causing the immobilization and precipitation of some elements such as iron, manganese, and zinc. This impact could be accelerated when soil salinity coincides with increases in soil pH (Maathuis and Diatloff 2013; Ramezanian 2013; Luo et al. 2015a, b, 2016; Kumar et al. 2016; Meier et al. 2017).

Soil salinity was and still one of the great threats facing the global food security. This soil salinity, caused by natural or anthropogenic factors, has been recognized as a serious challenge in land cultivation worldwide in arid and semiarid regions. Therefore, soil salinity could be considered an important abiotic stress causing a remarkable decrease in the crop production under saline soil conditions (Hasanuzzaman et al. 2013a, b). Concerning damage of salinization, soil salinization could lead to the disruption or alteration of the natural biochemical (Decock et al. 2015), biological (Smith et al. 2015), hydrological (Keesstra et al. 2012), and erosional (Berendse et al. 2015) Earth cycles. It is well reported that salt-affected soils constituent nearly 10% of the total global land (about 1 billion ha) including saline soils (Shahid et al. 2013). Soil salinity is distributed in more than 100 countries and widespread in all continents on the globe. Furthermore, saline soils are very common in arid and semiarid or desert and semidesert regions as well as may occur in different fertile alluvial plains. Thus, salt-affected soils include saline, sodic, and alkaline soils with high concentration of salt, sodium cation, and CO_3^{2-}as well as high pH in soil. Therefore, several studies have been published on the salinity of soils such as monitoring and mapping (e.g., Daliakopoulos et al. 2016; Guangming et al. 2017), management and reclamation of salt-affected soils (e.g., Arora et al. 2017), and use of marginal quality water in crop production (e.g., Shahid et al. 2013) and different mechanisms for plant salt tolerance (e.g., Almutairi 2016).

There are many commercial calcium products for amending sodic and saline-sodic soils. Generally, the function of these amendments is to provide soluble calcium and replace exchangeable sodium adsorbed on clay surfaces. The biological reclamation of salt-affected soils can be applied using organic materials, crop residues, and biofertilizers (Borde et al. 2017; Choudhary 2017; Singh and Jha 2017; Singh et al. 2017; Yadav et al. 2017b). These biological reclaimants could help in improving and maintaining the structure of soil, preventing erosion and supplying essential plant nutrients, and enhancing the biological activity in soils besides reclaiming sodic soils. New approaches could be also used in remediation of these salt-affected soils such as nanoremediation (Belal and El-Ramady 2016; El-Ramady et al. 2017; Libralato et al. 2017; Lofrano et al. 2017; Martínez-Fernández et al. 2017; Mitra et al. 2017; Saha et al. 2017).

Selenium (Se) and silicon (Si) are beneficial elements for higher plants (Swain and Rout 2017; Pilon-Smits et al. 2017). These elements have been recently used in alleviating the toxic effects of soil salinity (Habibi 2017; Sattar et al. 2017). Foliar selenium and silicon in combination or alone improved transpiration rate, water relations, photosynthetic attributes, chlorophyll contents, and the growth of wheat seedlings under stressed conditions. The reason of this increase is related to the accumulation of osmoprotectants (e.g., proline, soluble protein, and soluble sugar) and the increase in antioxidant enzyme activity (Sattar et al. 2017). These previous elements (Se, Si) also have been used in alleviating the oxidative stress of heavy metals such as cadmium (Cao et al. 2017a; Tang et al. 2015) and lead (Balakhnina and Nadezhkina 2017; Mroczek-Zdyrska et al. 2017), as well as their nanoparticles (Alsaeedi et al. 2017a, b).

Salt-affected soils suffer from a lot of troubles around the world such as a limited crop production due to their abiotic stresses particularly in arid and semiarid regions (Nan et al. 2016; Zhang et al. 2017a). Therefore, this review will focus on different roles of plant nutrients under soil saline conditions or salt-affected soils. The phytoremediation and management of these soils will be also highlighted.

13.2 Abiotic Stresses and Plants: Problems and Challenges

Generally, plants need some essential and/or beneficial nutrients in their growth and development as well as the proper environmental conditions. These ideal growth conditions sometimes could not occur, but different plant stresses may be dominated. These plant stresses include biotic and abiotic ones. The major plant abiotic stresses include high salinity; drought; cold and heat, which negatively impact on the survival; production of biomass; and yield of staple food crops up to 70% threatening the global food security (Mantri et al. 2012; Alshaal et al. 2017). Concerning plant stress, Springer has published more than 80 books about this subject including 6 books published during the last months of 2017 (e.g., Khan and Khan 2017; Mosa et al. 2017; Sarwat et al. 2017; Senthil-Kumar 2017; Sunkar 2017; Wu 2017). These books include some *hotspots* concerning plant stress such as using the integrated omics approaches in plant stress tolerance (Mosa et al. 2017), different new methods and protocols in plant stress tolerance (Sunkar 2017), the role of arbuscular mycorrhizas in plant stress tolerance (Wu 2017), the response of plant tolerance to individual and concurrent stresses (Senthil-Kumar 2017), and signaling of stress in plants using genomics and proteomics perspective (Sarwat et al. 2017).

The great challenge facing the scientific community is representing in the multiple or combined biotic and abiotic stresses on plants. That means not only one plant stress but also in general multiple stresses are facing plants. Plants face different environmental constraints (e.g., drought, pathogens, etc.), which do not always occur independently under field conditions and extreme weather patterns (Gupta and Senthil-Kumar 2017). Furthermore, several factors are controlling plant responses to combinations of stresses like the age of plants, how severe are the stresses, and the susceptibility of plants to pathogens. The shared plant responses include the common physiological and molecular levels, whereas the physiological traits could be dominants in case of individual stresses (Gupta and Senthil-Kumar 2017). The most common combined plant stress includes drought and salinity stress, which leads generally to a severe reduction in stomatal conductance, net photosynthetic rate, and enhanced oxidative damage (Gupta and Senthil-Kumar 2017). Plant responses to combined drought and pathogen infection (Gupta and Senthil-Kumar 2017) and drought and heat (Yadav et al. 2017a) have been also reported. Recently, a great concern toward the role and actions of plant nutrients in plant abiotic stress tolerance also has been issued (e.g., Hasanuzzaman et al. 2017).

Therefore, plant abiotic stresses have many problems and serious challenges. It is found that many beneficial plant nutrients have a distinguished role in the mitigation and protection of several crop plants against abiotic and biotic stresses such as silicon (Tripathi et al. 2014; Cao et al. 2017a), selenium (Domokos-Szabolcsy et al. 2017; Habibi 2017), and other essential elements like nitrogen (Khan et al. 2017), potassium (Ahanger et al. 2017; Kumar et al. 2017c), calcium (Huang et al. 2017; Nedjimi 2017; Sakhonwasee and Phingkasan 2017), zinc (ul Hassan et al. 2017; Upadhyaya et al. 2017), etc. Soil microbes (Mishra et al. 2017) or plant biostimulants (Van Oosten et al. 2017) also have a great role in the mitigation and protection of plants against stresses such as bacteria (Etesami and Beattie 2017; Li and Jiang 2017; Turan et al. 2017), mycorrhizal fungi (Borde et al. 2017; Huang and Wu 2017; Kumar et al. 2017a; Nath et al. 2017; Zhu et al. 2017), etc.

13.3 Soil Salinity: Problems and Challenges

According to many reports and due to salinity stress, about one-third of the global irrigated lands nearly is suffering from excess salinity causing a decrease in crop production every year worldwide (e.g., Tripathi et al. 2014; Naeem et al. 2017a). It is well known that salinity stress causes restricted plant growth and imbalance in cellular ions as a result from ion toxicity and osmotic stress. Crop production may be adversely impacted by salinity-induced nutrient deficiencies. Therefore, salinity stress is one of the major factors limiting the growth of plants and then the productivity of crops. Several studies have focused on the effects of soil and water salinity on a variety of crop plants including barley, cucumber, rice, tomato, wheat, etc. (e.g., Kim et al. 2017; Mohammadi et al. 2017; Shivakumar and Bhaktavatchalu 2017). Other investigations also have included the role of plant nutrients like Si and Se against different adverse effects of salinity confirming that these nutrients play a protective role against the salinity stress (e.g., Tripathi et al. 2014; Balakhnina and Nadezhkina 2017; Cao et al. 2017a; Habibi 2017; Sattar et al. 2017; Swain and Rout 2017; Tang et al. 2015).

Concerning the problems of soil salinity (Figs. 13.1, 13.2 and 13.3), these problems include (1) reduction in agricultural production, (2) low economic returns, (3) soil erosions, (4) limited water uptake from soils, (5) effects on soil physicochemical properties, (6) ion toxicity, (7) osmotic stress, (8) deficiency of some nutrients (e.g., N, Ca, K, P, Fe, and Zn), (9) oxidative stress on plants, (10) reduced plant phosphorus uptake due to precipitation of calcium phosphate ions, and (11) toxic effects of some elements like sodium, chlorine, and boron on plants (Shrivastava and Kumar 2015). Concerning the amelioration of soil salinity stress, a holistic

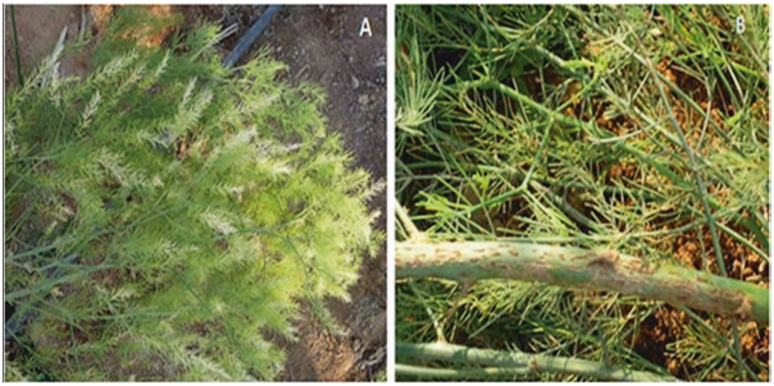

Fig. 13.1 Effect of soil alkalinity (pH: 8.9) and salinity of irrigation water (2500 ppm) on *Asparagus officinalis* plant in Wadi El Natrun, Beheira Governorate, where photo (**a**) represents salinity features on the leaves but photo (**b**) belongs salinity features on the shoot (Photos by Elmahrouk)

Fig. 13.2 Effect of soil alkalinity (pH: 8.7) and salinity of irrigation water (2500 ppm) on apricot plant in Wadi El Natrun, Beheira Governorate, where photos (**a**) and (**b**) represent early stage of salinity effect, (**c**) die of the terminal shoots, and (**d**) the end stage of salinity effect (Photos by Elmahrouk)

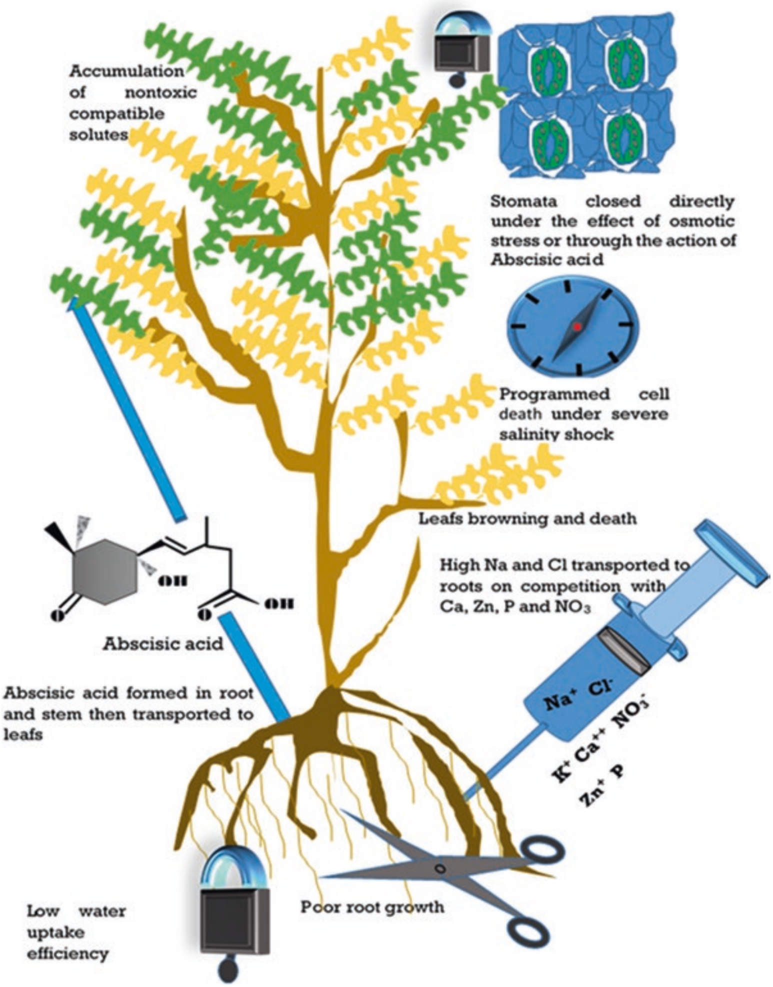

Fig. 13.3 Effect of soil salinity on plants includes many features such as decreased water uptake efficiency; poor root growth; decrease uptake of Ca, Zn, P, and NO_3; browning of leaves and death; closing of stomata and reduced photosynthesis process; and accumulation of nontoxic compatible solutes

approach should be applied toward the sustainability of the different soil amelioration methods. These approaches should have many benefits including the following points (Qadir et al. 2006; Choudhary 2017):

1. Sustainable: it should have a long-lasting, positive impact.
2. Simple: it should be easily manageable by farmers.
3. Efficient: it should be effective in action.
4. Low cost: it should need low capital input and should be inexpensive.

5. Enhancement of soil fertility: it should increase nutrient availability in soil.
6. Improve rhizosphere: it should improve soil chemical and physical properties.
7. Protect groundwater: it should avoid groundwater quality deterioration.
8. Compatible: it should be suitable for the biophysical environment.
9. Alleviate poverty: it should improve the well-being of the farming community.
10. Promote yield: it should increase the productivity of crops.
11. Conserve environment: it should improve the environment and sequester carbon.
12. Replenish soil: it should restore soil and increase the land's value.

Therefore, soil salinity is a serious global problem facing the arid and semiarid regions. This problem needs a holistic approach to ameliorate and mitigate it. The distinguished features resulting from the soil salinity in arid and semiarid zones are very common. Hence, the new approaches including biological and nanomaterials should be used in seeking sustainable development. The great challenge facing the universe is that more than 50% of the arable lands by the year 2050 will be salinized as reported by Naeem et al. (2017b). So, the researchers should search about unconventional solutions to overcome and mitigate different risks resulting from this challenge.

13.4 Role of Plant Nutrients in Ameliorating Soil Salinity Stress

Plant nutrients not only give the plants the full power during entire life but also help plants in ameliorating different stresses including abiotic and biotic. The salinity stress affects nearly all plant development aspects starting from the germination of seeds, enzyme activity, vegetative growth, the protein synthesis and mitosis of DNA and RNA, as well as reproductive development (Horie et al. 2012; Naeem et al. 2017b). Concerning plant salinity tolerance, plants have several multifaceted physiological aspects involving the adaptation to signaling and metabolic networks. Plants also can use many mineral nutrients (like N, Ca, Si, and Se) in their facing tolerance mechanisms against different environmental challenges (Khan and Basha 2016; Naeem et al. 2017b).

Concerning effects of soil salinity on the nutrition of plants, nutrient plant disturbances reduce the growth of plant through affecting the transport and partitioning of different nutrients. Soil salinity also may cause deficiencies or imbalances in plant nutrients, due to the competition of Na^+ and Cl^- with many plant nutrients such as Ca^{2+}, K^+, and N-NO_3^-. A distinguished reduction in plant growth may occur under saline conditions due to specific ion toxicities (e.g., Na^+ and Cl^-) and ionic imbalances (Alshaal et al. 2017; Forni et al. 2017). Furthermore, increased NaCl concentration has been reported to induce increase in Na and Cl as well as decrease in N, P, Ca, K, and Mg level in many studied plants like medicinal legumes (Naeem et al.

2017b) for sustainable crop production under salinity stress (Singh et al. 2017; Sharma and Singh 2017). Because of these effects, it is vital that Zn, K, P, and N nutrition are monitored as they may limit plant growth in a saline soil. Therefore, application method of fertilizers must be chosen carefully to be an efficient way of combating sodium-induced stress (Negm and Eltarabily 2017; Tei et al. 2017).

Many fertilizers contain soluble salts in high concentrations. Therefore, the nutrient source, rate, timing, and placement are important considerations in the production of all crops. Muriate of potash or KCl, as a common K-fertilizer, is unsuitable for saline soil, whereas nitrate can eliminate effects of high chloride concentrations in soil and water. Salt indices for most commercial fertilizer products have been reported. For example, KCl has a salt index 205 times more that of K_2SO_4. Band application of fertilizers with high salt indices generally should be avoided near seedlings. It could preclude sodium accumulation on the soil's exchange complex by applying gypsum as well as maintain soil structure and improve water infiltration (Sharma and Singh 2017). The role of some plant nutrients in ameliorating soil salinity stress such as silicon and selenium as well as their nanoparticles will be highlighted in the following subsections.

13.4.1 Soil Salinity and Silicon

Silicon is known to be the seocnd element after oxygen in its occurrence in the Earth 's crust (28%). It is also a metalloid element, and in compound form it occurs as SiO_2 or silicon dioxide (Swain and Rout 2017). Silicon did not confirm as essential nutrient for higher plants in spite of a lot of crucial roles in plants (Tables 13.1 and 13.2). It has been demonstrated that the application of silicon is beneficial for plant growth, development, and yield of several plants as well as the alleviation of different plant stresses including nutrient imbalance (Swain and Rout 2017). Therefore, the application of silicon under either drought or salt stress has increased the quality of straw and grain yield as well as biomass, plant growth, and photosynthetic pigments. Silicon also has a vital role in the stimulation of antioxidant enzymes and gene expression in plants, modification of gas exchange attributes, regulation of the synthesis of compatible solutes, and osmotic adjustment under both salt and drought stress. In addition, the application of silicon also decreases the uptake and translocation of Na^+ as well as increases the uptake and translocation of K^+ under salinity stress. However, these previous mechanisms vary with duration of stress imposed, growth conditions, plant species, genotype, and so on (Qados 2015; Swain and Rout 2017).

Concerning silicon and soil salinity, a clear role of Si has been documented in inducing the plant growth under abiotic stresses in particular soil salinity (e.g., Balakhnina et al. 2015; Garg and Bhandari 2016). It is indicated that most of the beneficial effects of Si under salinity stress may have resulted from reducing the uptake and translocation of Na^+ and Cl^- to shoots and maintaining plant-water relations, which in turn contributes to salt dilution and then improving yield compo-

Table 13.1 A comparison between selenium and silicon according to some selected properties of some physical, chemical, and biological properties

Properties or items (unit)	Silicon (Si)	Selenium (Se)
Name origin	From the Latin word *silex* (flint)	From Greek word *Selênê* (moon)
Discovery year and discoverer	J. J. Berzelius (1824)	J. Berzelius (1817)
World mine production in 2016 according to USGS (2017)	7200,000 mt	2200 mt
Abundance in the Earth's crust	28%	0.05 (mg kg^{-1})
Abundance or usual soil content	54%	0.33 (mg kg^{-1})
Abundance ranking order in earth crust	2	69
Most important minerals	Kaolinite $Al_2(OH)_4Si_2O_5$ Serpentine $Mg_3(OH)_4Si_2O_5$	Klockmannite (CuSe), clausthalite (PbSe), tiemannite (HgSe)
Most important sources	Quartz, clay, and all silicate minerals	Refining of lead, copper, nickel
Most important uses	Transistors, computer chips, solar cells, electronics, alloys	Photoelectric cells, TV cameras
Common valence states	+2,+4, −4	−2, 0, +2,+4, +6
Ionic radius (A°), where 1 Å = 100 pm	0.21	0.50
Electronegativity (according to Pauling scale)	1.90	2.55
Atomic number	14	34
Atomic mass (atomic mass unit)	28.08	78.96
Atomic radius (picometres or pm)	117	122
Density at 20 °C (g cm^{-3})	2.33	4.79
Boiling point (°C)	3265	684.9
Melting point (°C)	1410	217
Crystal structure	Cubic	Hexagonal
Principal forms for plant uptake	H_4SiO_4 or $Si(OH)_4$	SeO_4^{2-} or SeO_3^{2-}
Essentiality for animals and plants	Suggested and beneficial	Essential for animals and beneficial for plants
Critical or sufficient level in plant leaf (DW)	<0.5% most species	0.1–2.0 (mg kg^{-1})
Toxic level in plant leaf (DW)	More than 10% in rice	5.0–30 (mg kg^{-1})
Uptake by plants	Passive in mono silicic acid (H_4SiO_4) or amorphous silica	Passive (SeO_3^{2-}) and active for (SeO_4^{2-}) and selenomethionine

Table 13.2 The common cited beneficial effects of both silicon (Si) and selenium (Se) on plants under stress

Role of Si and Se under plant stress	Example for cited references	
	Silicon (Si)	Selenium (Se)
Enhancement of plant growth and yield	Swain and Rout (2017)	Shahzadi et al. (2017) and Schiavon et al. (2017)
Resistance to herbivores and parasitism	Nikpay et al. (2017)	Reynolds et al. (2017) and Schomburg and Arnér (2017)
Drought stress	Rizwan et al. (2015), Ma et al. (2016), Ouzounidou et al. (2016), Cao et al. (2017b), and Zhang et al. (2017b)	Nawaz et al. (2015) and Schiavon et al. (2017)
Salinity and water stress	Rizwan et al. (2015), Ouzounidou et al. (2016), Sattar et al. (2017), Xu et al. (2017), and Zhang et al. (2017b)	Habibi (2017), Sattar et al. (2017), and Shahzadi et al. (2017)
Oxidative stress	Hasanuzzaman et al. (2017) and Li et al. (2017)	Balakhnina and Nadezhkina (2017) and Mechora et al. (2017)
Plant diseases or biotic stress	Rodrigues and Datnoff (2015) and Klotzbucher et al. (2017)	El-Ramady et al. (2016)
Alleviation the toxicity of lead	Balakhnina and Nadezhkina (2017), Mroczek-Zdyrska et al. (2017), and Li et al. (2017)	Balakhnina and Nadezhkina (2017) and Mroczek-Zdyrska et al. (2017)
Cadmium	Cao et al. (2017a) and Tang et al. (2015)	Schiavon et al. (2017)
Improve plant-nutrient balance	Swain and Rout (2017)	Hasanuzzaman et al. (2017)

nents (Garg and Bhandari 2016). As reported, saline soils or presence of excessive amounts of salt could lead to osmotic, oxidative, and ionic stress on plants (Sattar et al. 2017). Therefore, many features could be occurring under oxidative stress, including peroxidation of lipids and excessive accumulation of reactive oxygen species like hydrogen peroxide and superoxide anion that tends to damage proteins, lipids, and nucleic acids (Soundararajan et al. 2017). Several studies have been published to focus on the relation between silicon and its role under soil salinity (e.g., Farooq et al. 2015; Garg and Bhandari 2016; Sattar et al. 2017; Soundararajan et al. 2017; Swain and Rout 2017; Zhang et al. 2017b).

Therefore, it could be concluded that many approaches have been used in alleviating the negative effects of salt stress in several crops. Proper plant nutrition is one of the most important strategies to alleviate this salt stress in crop production. Mineral nutrient supply to plants also plays a critical role in improving tolerance potential of plants against various environmental stresses including salinity, drought, disease, temperature, etc. Reducing uptake of sodium and chloride by plants is the common mechanism of salt tolerance in plants as well as a distinguished role of potassium. The role of nitrogen also is very important under soil saline conditions due to the accumulating of organic N-compounds in plants. These organic N-compounds include all amino acids in protein and a number of nitrogen-containing compounds such as amino acids (proline and glycine betaine), amides, and polyamines. Thus, exogenous application of N-fertilizers may reduce the effect of salinity and enhance the growth of plants. Silicon also has the same action in ameliorating the salt stress.

13.4.2 Soil Salinity and Selenium

No doubt that selenium is an essential micronutrient for many living organisms including bacteria, some algae, archaea, and animals. However, the essentiality of Se in the metabolism of plants and fungi still needs more proofs. Selenium in the form of selenocysteine (SeCys) or selenoproteins is the main essential form required for the survival of organisms like humans. These selenoproteins have main functions including redox functions, immune function through thyroid metabolism, and spermatogenesis (El-Ramady et al. 2016; Pilon-Smits et al. 2017). Under high levels of Se, it becomes toxic to living organisms due to the replacement of S-amino acids in proteins by their Se-analogs causing an oxidative stress. Therefore, the main problem of Se is represented in the very narrow window between adequacy and the large variations in dietary Se intake (˂40 μg/day) and toxicity (˃400 μg/day) for humans and animals (dos Reis et al. 2017; Dhillon and Bañuelos 2017). Thus, several symptoms of both Se toxicity and deficiency are prevalent worldwide. Concerning the essentiality of Se for higher plants, it is confirmed that selenium is a beneficial nutrient enhancing plant growth and antioxidant activity (Table 13.2). Higher plants have the ability to uptake selenium using sulfur transporters because organic Se-compounds are analogous to S. Some plant hyperaccumulators could accumulate Se in high levels (0.1–1.5% of their dry weight). This reflects the great concern for animal, human, and environmental health (Pilon-Smits et al. 2017).

Several methods are in progress to ameliorate salinity stress such as use of selenium, which is considered as an essential trace element for some microbes, animals, and humans, but its essentiality for plants is yet to be proved as mentioned before (Table 13.1). At a low level of concentration, Se imparts diverse beneficial effects and stimulates growth as well (e.g., Domokos-Szabolcsy et al. 2017; Habibi 2017; Kiryushina and Voronina 2017; Schiavon et al. 2017). Previous studies indicate that the presence of Se in the growth medium can provide partial protection from the effects of some abiotic stresses such as drought (Hasanuzzaman and Fujita 2011; Nawaz et al. 2015; Schiavon et al. 2017), salinity (Habibi 2017; Sattar et al. 2017; Shahzadi et al. 2017), high temperature (Hasanuzzaman et al. 2014a), toxic metals (Balakhnina and Nadezhkina 2017; Mroczek-Zdyrska et al. 2017), and oxidative damage (Balakhnina and Nadezhkina 2017; Mechora et al. 2017). Therefore, most of the beneficial effects of Se have been attributed to reduction in oxidative stress by increasing the activity of antioxidants Balakhnina and Nadezhkina 2017; Mechora et al. 2017). Previous studies also reported about many protective effects of Se for plants grown under salt-stressed conditions (e.g., Hasanuzzaman et al. 2017).

Therefore, it could be concluded that the distinguished role of Se in ameliorating the plant environmental stress still needs more elucidation about the specific mechanisms of Se-mediated adaptation to salt stress. Regarding the positive effects of Se in improving plant tolerance to salt stress, these responses include (1) enhancing plant growth, (2) increasing the accumulation of photosynthetic pigments and compatible solutes, and (3) activating antioxidant machinery. These previous responses depend on various plant physiological and metabolic changes. These changes, in turn, start from seed germination to final crop harvest. Further studies are needed for more emphasis to confirm the essentiality of Se for higher plants as well as the mode of action of the ameliorative action of Se in plants under stress.

13.4.3 Nano Selenium and Nano-silica Under Soil Salinity

The universe definitely faces several global problems including climate change, environmental pollution, food security, soil security, energy and water crisis, etc. These previous challenges represent a serious stress on the global bio-resources. Environmental pollution, drought, salinity, temperature, and flooding are the most important abiotic stresses facing the global crop production (El-Ramady et al. 2017). New and modern approaches have been successfully used in the mitigation and adaptation of these previous stresses particularly the nanotechnology. Several nanoparticles and nanomaterials have been also applied in agricultural sectors (Belal and El-Ramady 2016; Shalaby et al. 2016; Saratale et al. 2017) including almost all fields such as plant nutrition (e.g., Dimkpa et al. 2015; Subramanian et al. 2015; El-Ramady et al. 2017; Jampílek and Kráľová 2017; Subramanian and Thirunavukkarasu 2017); plant protection and nanopesticides (e.g., Chhipa and Joshi 2016; Kumar et al. 2017b); nanosensors for food and agriculture (e.g., Singh 2017; Srivastava et al. 2017); soil and water nanoremediation (e.g., El-Ramady et al. 2017; Sangeetha et al. 2017), against environmental stress (e.g., Wang et al. 2015; Emadi et al. 2016; Mahdy et al. 2017; Mansouri et al. 2017; Rameshraddy et al. 2017); etc.

There is no any agricultural sector untouched by nanotechnology nowadays. This penetration of nanotechnology includes the new tools for rapid detection of diseases, molecular treatment of plant diseases, and enhancing the ability of plant to absorb nutrients. This nanoscience also aims to increase the fertility of soils and crop production in spite of the potential of nanotechnology is yet to be fully exploited in management and cultivating of salt-affected soils (Ibrahim et al. 2016; Patra et al. 2016). Concerning the application of nanotechnology under saline soil conditions, it is in the infant stage and needs more researches and investigations. However, some studies have been published regarding the role of nanomaterials of silicon and selenium as well as other metals under salt-affected soils (e.g., Patra et al. 2016; Alsaeedi et al. 2017a, b; El-Ramady et al. 2015a, b, 2016; Lofrano et al. 2017). So, the nanotechnology could be used in developing reclaimants more efficiently and readily manufacturable. These nanoparticles including carbon and zeolite nanoparticles (a polymer carrier), calcium compounds in nanoscale, as well as biochar can act as exchange sites for binding Na^+ and thus reduce the adverse effects like clay dispersion and swelling (Patra et al. 2016).

Organic forms of selenium and some salts have been used in studying its biological effects for years. Elemental selenium (Se^0) nanoparticles or selenium nanoparticles (SeNPs) have gained some attention recently as a possible source of this beneficial component (El-Ramady et al. 2015a, b, 2016). It is found that the range of 5–200 nm of selenium nanoparticles plays an important role as a vital size for nanoparticles. Also, the transmission electron micrograph (TEM) of the separated Se nanoparticles showed the spherical shape in the range of 80–220 nm in size and the antioxidant properties as reported by Prasad et al. (2013). It is confirmed that Se nanoparticles have a low toxicity and high biological activity as well as an excellent bioavailability (El-Ramady et al. 2016). Therefore, SeNPs are gaining importance in electronics and optics due to their enhanced photoconducting, semiconducting, catalytic, and photoelectrical properties (Srivastava and Mukhopadhyay 2013). Se nanoparticles exhibit low cytotoxicity compared with selenium compounds and possess many medicinal applications as excellent anticancer and therapeutic activities (Forootanfara et al. 2013; Bhattacharjee et al. 2017). Selenium is essential (as a cofactor) for many enzymes in animals such as glutathione peroxidases and thioredoxin reductase. Thus, these previous enzymes are supplied in meals of animals. However, some studies have shown that Se nanoparticles have the efficiency compared with organic and inorganic selenium compounds (Benko et al. 2012; Hu et al. 2012; El-Ramady et al. 2016).

The biological roles of Se nanoparticles and their biosynthesis in plants have been involved in several studies (e.g., Domokos-Szabolcsy 2011; Domokos-Szabolcsy et al. 2012; El-Ramady et al. 2014c, 2015a, b, c, 2016; Srivastava and Mukhopadhyay 2015; Mykhaylenko and Zolotareva 2017). Furthermore, several applications of Se nanoparticles have been listed in both biological and nanotechnological fields including (1) new chemopreventives (Zhang et al. 2008), (2) the development of safer selenium vitamins and food additives (Hnain et al. 2013), (3) novel antibiotic coatings (Wang and Webster 2012), (4) anticancer treatments (Kong et al. 2011), and (5) in vivo fluorescent dyes for bioimaging applications (Gu et al. 2012).

It is worth to mention that there is a great chance for nano-Se and nano-silica use in fertilization and plant nutrition fields under stress. Many studies have proven that these nano-fertilizers (nano-Se and nano-silica) play an important role in increasing the yield of many crops and then food security (Liu et al. 2015; Mastronardi et al. 2015; Wang et al. 2015, 2016; Karimi and Mohsenzadeh 2016; Alsaeedi et al. 2017a, b). The biological and physiological effects of nano-Se on different crops have been presented such as tobacco (Domokos-Szabolcsy 2011; Domokos-Szabolcsy et al. 2012), rice (Premarathna et al. 2010), tomato (Haghighi et al. 2014), and giant reed (Domokos-Szabolcsy et al. 2014). Thus, selenium nanoparticles have the ability to stimulate the regeneration of roots under higher concentrations (more than 100 mg L^{-1} nano-Se) with significant increase in the fresh weight.

Concerning nano-silica, it has a distinguished role in the mitigation of salinity stress and counteraction of the negative effects of salt on plant growth. It is reported that nano-silicon application can improve the germination of seeds and the growth of seedlings of some plants like tomato, maize (Suriyaprabha et al. 2012), and common bean or *Phaseolus vulgaris* L (Alsaeedi et al. 2017a). Also, the role of nano-silica in alleviating salt and drought stress of some plants like Glycyrrhiza uralensis (Zhang et al. 2017b), tomato (Almutairi 2016), and common bean (Alsaeedi et al. 2017b). As mentioned before, silicon depositions in the tissues help to alleviate water stress by reducing transpiration rate, improve light interception characteristics by keeping the leaf erect, increase resistances to diseases pests and lodging, and remediate nutrient imbalances, and there are other documented beneficial effects (Zhang et al. 2017b). Nano-silicon also was used to improve salinity tolerance of sweet pepper plant, where it was estimated that 1.0 g of silica nanoparticles having size of 7.0 nm diameter exhibit wide absorption surface equal to 400 m^2. Furthermore, silica nanoparticles also exhibit its effect on xylem humidity and water translocation and enhance turgor pressure; thus, leaf relative water content and water use efficiency will be increased in plants. Siddiqui and Al-Whaibi (2014) confirmed that the application of nano-SiO_2 has many benefits under stress including reducing the rate of chlorophyll degradation and increasing stomatal conductance, the net photosynthetic rate, transpiration rate, and water use efficiency. Nano-SiO_2 particles are absorbed better and faster than micro-SiO_2, Na_2SiO_3, and H_4SiO_4 when applied on root of maize and seeds; because of fast absorption of nanoparticles, they can be immediately utilized by plants to fulfill their growth needs (Suriyaprabha et al. 2012). The effect of nano-silicon application on the expression of salt-tolerant genes in germinating tomato (*Solanum lycopersicum* L.) seedlings under salt stress is also studied, where four salt stress genes, *AREB*, *TAS14*, *NCED3*, and *CRK1*, were upregulated by nano-Si under salt stress and six genes, *RBOH1*, *APX2*, *MAPK2*, *ERF5*, *MAPK3*, and *DDF2*, were downregulated. These results suggest that nano-Si has the ability in moderating inhibition in the germination of seeds and the growth of plants under saline environments (Almutairi 2016).

Therefore, it could be concluded that both nano-selenium and nano-silicon have distinguished roles in alleviating the detrimental effects of Na^+-derived salinity on germination and growth of many crops. These findings generally could be reinforced by low Na content which was measured in plant tissues after treating seedlings with 300 mg L^{-1} or 100 mg kg^{-1} of nano-silicon and nano-selenium for common bean and most crops, respectively.

13.5 Phytoremediation of Soil Pollution Under Saline Conditions

It is well known that several human activities have led to environmental humungous load of pollutants day by day. These pollutants already have created imbalance in the environmental equilibrium (El-Ramady et al. 2015a, b; Bauddh et al. 2017; Chakravarty et al. 2017). Therefore, several approaches or mechanisms of

Table 13.3 Some common plant species have the ability to phyto-remediate some pollutants

Contaminant	Plant species
Arsenic	*Pteris vittata* L.
Cadmium	*Oryza sativa* L.
Chromium	*Brassica juncea* L.
Copper	*Elsholtzia splendens*
Lead	*Chenopodium album* L.
Mercury	*Marrubium vulgare*
Nickel	*Alyssum lesbiacum*
Selenium	*Brassica rapa* L.

remediation have been used in remediation of soil and water. These approaches include physicochemical (excavation, landfilling, thermal treatment, leaching, and electro-reclamation) and biological remediation including bio- and phytoremediation (Anjum et al. 2017a, b; Purakayastha et al. 2017). Comparing with traditional techniques, phytoremediation (using plants in clean up polluted soil and water) could be considered more cost-effective and environmentally beneficial pathways in restoration of polluted sites (Bauddh et al. 2017). Many mechanisms have been successfully adapted in phytoremediation including phytodegradation, phytoextraction, rhizofiltration, phytostabilization, and phytovolatilization of contaminants in the polluted sites (e.g., Anjum et al. 2017c; Dhillon and Bañuelos 2017; Purakayastha et al. 2017; Srivastava 2017; Sarkar 2018b). Several botanical species have been used in remediating the contaminated sites and this is confirmed by many researchers. Many crop plants including medicinal plants, bioenergy crops, trees, and weeds already have been found to be the best options for phytoremediation (Bauddh et al. 2017; Chakravarty et al. 2017). Some important hyperaccumulator plants (1000 mg kg^{-1}) used for phytoextraction of some heavy metals in soils as reported by Purakayastha et al. (2017) are listed in Table 13.3.

It is known that salt-affected soils could be defined as soils with high levels of dissolved salts (EC more than 4 dS m^{-1}) and/or high concentrations of exchangeable or adsorbed sodium ions (SAR and ESP less than 13 and 15, respectively) in the soil matrix. These soils suffer from soil salinity and sodicity, causing losses in crop yields in many regions worldwide especially in arid and semiarid zones (Hasanuzzaman et al. 2014b; Purakayastha et al. 2017). Amelioration of salt-affected soils could be performed using soil chemical amendments like gypsum and other applications of organic fertilizers (e.g., compost, manure, and green manure crops) and halophytes (Purakayastha et al. 2017). An increased concern about phytoremediation of saline soil conditions or salt-affected soils as a *hotspot* has been recorded nowadays. So, several investigations have been published regarding phytoremediation of salt-affected soils (e.g., Arora and Rao 2017; Arora et al. 2017; Bharti et al. 2017; Gerhardt et al. 2017; Purakayastha et al. 2017; Yadav et al. 2017b).

The most important new approaches used in phytoremediation include nanomaterials and nonfood bioenergy crops. So, several books recently have been published by Springer regarding the phyto- and bioremediation (e.g., Anjum et al. 2017a, b; Ansari et al. 2017; Arora et al. 2017; Bauddh et al. 2017; Kalia and Kumar 2017; Mehnaz 2017; Prashanthi et al. 2017; Sarkar 2018a). Therefore, phytoremediation is an economical and effective method of reducing or removing pollutants in salt-affected soils. So, halophytes could be used as a cost-effective and environmentally sound green technology in phytoremediation of salt-affected soils (i.e., saline and sodic soils). Furthermore, it could be used salt-tolerant plant (e.g., grass and biofuel species) in multipurposes under alkaline soil conditions such as in bio-amelioration of degraded agricultural and wastelands (Singh et al. 2016). Under gas and oil mining conditions, a huge number of halophytic grasses have been proven to be effective in revegetating brine-contaminated soils (Arora and Rao 2017).

Concerning the halophytes (salt-loving, salt-tolerant, or saltwater plants), it could be defined as tolerant plants that grow in high salt concentrations, which kill 99% of other species or adapted plants that grow well in high salinity conditions (Arora and Rao 2017; Purakayastha et al. 2017). In other words, halophytes could be defined generally as rooted seed-bearing plants (i.e., succulents, grasses, shrubs, herbs, and trees), which grow in a wide variety of salt marshes and mudflats to inland deserts, saline habitats from coastal sand dunes, salt flats, and steppes. Halophytes could be also divided based on their occurrence into hydro-halophytes (plants are growing in saline water medium) and xero-halophytes, which grow mainly in dry land saline conditions (Arora and Rao 2017). Some halophytes under environments are listed as follows as reported by Arora and Rao (2017):

1. Halophytes of oil-yielding species: *Salicornia bigelovii*, *Salvadora persica*, *S. oleiodes*, *Terminalia catappa*, and *Calophyllum inophyllum*
2. Coastal halophyte plants: *Borassus flabellifer*, *Calophyllum inophyllum*, *Pongamia pinnata*, and *Nypa fruticans*
3. Petro-crops: *Jatropha curcas* and *Euphorbia antisyphilitica*
4. Medicinal plants: *Plantago ovata*, *Adhatoda vasica*, *Withania somnifera*, and *Cassia angustifolia*
5. Food-yielding halophytes: Sugar beet (*Beta vulgaris* L.), date palm (*Phoenix dactylifera*), guava (*Psidium guajava*), Java plum (*Syzygium cumini*), and pomegranate (*Punica granatum*)
6. Nitrogen-fixing halophytes: *Albizia*, *Cassia*, *Cyamopsis*, *Leucaena*, *Pongamia*, *Sesbania*, and *Trifolium*

Therefore, phytoremediation of soil pollution under saline conditions is an important green technology that could be used in reclamation of polluted and salt-affected soils. This phytoremediation process depends on phytoremediator plants, fertilization of soil, and kind of soil amendments (chelating agents) under saline soil conditions. It could be concluded that several economic and useful halophytes have the effective capacity in bio-amelioration of salt-affected soils. These plants also have a great capability in removing substantial quantities of salts and producing higher biomass, thereby improving these soils.

13.6 Conclusion

Plant nutrients including essential and beneficial play several crucial roles in metabolic, molecular, physiological, ecological, and evolutionary aspects as well as regulatory processes in plants. These plant nutrients have a pronounced impact on entire plant life including plant growth and its development as well as the regulatory role of mineral nutrients under stresses. These plant nutrients should be applied for plant nutrition in a proper or right amount, time, form, and dose (or known as 4R nutrient stewardship: right fertilizer source, right rate, right time, and right place). An ameliorative effect of plant nutrients has been recorded on the plant growth and productivity under different abiotic and biotic stresses. These plant stresses are the main limiting factors of crop yields causing losses of billions of dollars annually all over the world. Several plant nutrients have proven and confirmed their roles in ameliorating stress such as nitrogen, potassium, sulfur, selenium, and silicon. Different plant cellular, physiological, and molecular strategies already have been used under unfavorable or stress conditions. Under saline soil conditions, various plant responses have been recorded in plant adaptation to this stress such as osmotic regulation, hormone metabolism, controlling ion uptake, transport and balance, antioxidant metabolism, and stress signaling. Therefore, further studies are needed for more understanding and to emphasize about the plant response to stress conditions and its adaptation to different changing environments at the molecular level. The study of intracellular and intercellular molecular interaction involving the response of these plants toward soil salinity stress is also an urgent issue.

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Chapter 14
Ionic Basis of Salt Tolerance in Plants: Nutrient Homeostasis and Oxidative Stress Tolerance

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Abstract Salinity, recognized as a major threat in agriculture, causes 4.0–6.3% yield loss annually across the world. The problem is aggravated due to increasing irrigation with suboptimal quality of irrigation water and more salinization of coastal area due to the rise in sea level because of climate change. In saline soil, excessive concentrations of Na^+ and Cl^- impair absorption of other beneficial ions such as K^+ and Ca^{2+} that in turn inhibit plant growth and productivity. Maintenance of cellular K^+ level and K^+/Na^+ ratio is still considered the most important factor for salt tolerance. Under high-Na^+ environment, excess Na^+ competes with K^+ thereby hindering its uptake. Tolerant plants by employing a number of strategies restrict Na^+ movement to young meristematic tissues and allow greater movement and/or tissue retention of K^+ to physiologically more active tissues. Under salt stress different K^+- and Na^+-specific transporters, viz. SOS, NHX, and HKT family transporters (regulate cellular Na^+ movement) and HAK, AKT, KT, and KUP (regulate K^+ movement), either by upregulation or downregulation, control the cellular ion homeostasis and salt tolerance in plants. SOS1, a plasma membrane-bound Na^+/H^+ antiporter, mostly active in root tissue, removes the excess salt from the plant body by pumping them back to the rhizosphere in an energy-dependent process. Tonoplast-bound vacuolar Na^+/H^+ antiporters (NHX family transporters) play crucial role in Na^+ compartmentalization inside the vacuole in mature cell in both root and leaf tissues. Storing excess salts in vacuole imparts tolerance in multifaceted manner, viz.

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imparting tissue and osmo-tolerance. Biosynthesis of organic osmolytes, a more energy-expensive process, is sometimes substituted by the accumulation of excess Na^+ in non-active tissues under salt stress. Improved Ca^{2+} status inside the plant tissue is another important factor associated with salt tolerance and acts as a key signalling molecule to initiate Na^+ exclusion. Several QTLs and miRNAs were reported to impart salt tolerance in several crops. Managing salinity beyond crop improvement strategies was also deliberated, e.g. lowering salt effect through K^+ supplementation and phytohormones, etc. In this compilation, emphasis has been given on how nutrient/ionic imbalance causes deleterious effects on plants under saline conditions and what are the possible adaptive strategies plants employ to maintain the ionic homeostasis in saline environment.

Keywords Salinity · Na^+-K^+ transporter · Osmolytes · Tissue tolerance · ROS detoxification · Salt overly sensitive (SOS) pathway

14.1 Introduction

In the last few decades, we witnessed substantial increase in productivity of food grains, oilseeds, pulses and cash crops mostly through adoption of intensive agriculture, viz. high-yielding varieties, precise fertilizer and nutrient management practices, more efficient crop protection measures, etc. But, with the continuous increase in global population by every passing year, there is an estimated need to produce 87% more food crops such as rice, wheat and maize by 2050 over that we are producing today (FAO 2017). As the horizontal area expansion in fertile agricultural land almost came to a saturation in most countries, there is a current shift in encompassing more and more nontraditional areas under cultivation to cater the global food demand. Despite the much advancement in agricultural science in all over the world, abiotic stresses still cause havoc on cultivation due to its widespread and unmanageable nature, including salinity, drought, heat and cold, critically threaten crop production and result in substantial yield loss in large arable land worldwide. Among these, soil salinity is one of the prime environmental constraints to crop production and is further expected to increase due to global climate changes (increase in coastal salinity mainly due to the rise in mean sea level) and as a consequence of injudicious and/or faulty irrigation practices. As per the recent estimate, about 800 million hectares of land globally is affected by salinity (FAO 2017). On an average 2,000 ha of irrigated land across 75 countries has been degraded by excess salt annually owing an estimated economic loss in the tune of US$ 12 billion (Ghassemi et al. 1995).

Soil salinization is a worldwide problem for agriculture affecting 6% of total Earth's land, as a result of natural accumulation over long periods of time (Rengasamy 2002). However, agricultural activity contributes to secondary salinization: 2% of all dry land is becoming salinized, and more than 20% of irrigated soils are affected, mostly because of irrigation water containing small amounts of sodium chloride (Tester and Davenport 2003). Saline soils in general affect plant growth negatively and may even have a lethal effect causing programmed cell death upon extended exposure to high salinity. Based on the ability to tolerate NaCl concentrations, plants can be classified into two groups: glycophytes or salt-sensitive species (which are unable to tolerate even mild levels of salinity for longer periods of time) and halophytes or salt-tolerant species (which are capable of growing and thriving under high salinity). Primarily, excess salt in the soil decreases the water potential in the rhizosphere region, rendering plants unable to absorb water even in the absence of actual limitation of water quantity, a soil condition termed as physiological drought. As a result, many plant processes, viz. at the cellular level including cell enlargement, cell division, cell wall properties, etc., as well as various leaf parameters such as colour, succulence, necrosis, etc., and at whole-plant level, shoot/root ratio, growth and yield get affected (Hasegawa et al. 2000).

For most of the glycophytes, highly saline growing environment adversely affects the germination process, plant growth and metabolism as well as the overall physiology by causing ionic and osmotic stresses (Iterbe-Ormaetxe et al. 1998). Salt stress is often noted as a causal factor for increased respiration rate and ion toxicity while subsequently altering the C and N metabolism in plant cell (Kim et al. 2004). Additionally, mineral distribution and membrane instability (Marschner 1986) along with permeability (Gupta et al. 2002) and decreased biosynthesis of chlorophyll pigments and photosynthetic inefficiency (Munns 2002), all of which are caused by salt stress, collectively lead to impaired economic crop productivity. Stress-induced build-up of sugars and other compatible organic solutes is a common phenomenon for most of the abiotic stresses including soil salinity. They can serve as osmoprotectants, thus helping in stabilizing biomolecules under stress conditions. Although accumulation of ions for osmotic adjustment is energetically more preferable, many plants accumulate organic osmolytes (proline, betaine, polyols, sugar alcohols and soluble sugars) to counteract osmotic stresses. Both glycine betaine and trehalose serve as major osmoprotectants which stabilize the quaternary structures of proteins and highly ordered cellular and intracellular membranes. Proline acts as a sink for carbon and nitrogen and scavenger of free radical, which stabilizes subcellular structures (membranes and proteins) and maintains cellular redox potential (Reviewed in Chakraborty et al. 2013).

Salt stress also induces accumulation of reactive oxygen species (ROS), causing oxidative damage to cellular macromolecules, viz. proteins, membrane lipids and nucleic acids. Detoxification of these ROS is absolutely essential for plants to survive under salinity stress. To counterbalance the ROS production and oxidative stress, plants produce either molecular antioxidants for direct scavenging of these ROS or detoxify them via coordinated network of antioxidant enzymes, viz. superoxide dismutase, catalases, peroxidases and enzymes of ascorbate-glutathione cycle. Under various abiotic stresses, the activity and expression levels of genes encoding ROS-detoxifying enzymes were reported to be enhanced by oxidative stress (Abogadallah 2010; Chakraborty et al. 2016a).

Ionic homeostasis or regulation of Na^+/K^+ balance inside metabolically active tissue is still considered to be the most important criteria for salt tolerance (Munns and Tester 2008). Exposure to higher levels of salt stress, particularly NaCl, affects uptake of water and dissolved nutrients resulting in impaired plant water status and creates ionic imbalance by means of the cellular accumulation of toxic Na^+ and Cl^- ions. Sodium ions if accumulated in the cytoplasm can become extremely toxic to living cells showing their adverse effects on K^+ nutrition and other pivotal plant physiological mechanisms like activity of cytosolic enzymes, photosynthesis and metabolism (Shabala and Cuin 2008; Degl'Innocenti et al. 2009). Besides, salt stress heavily tolls on the ionic homeostasis of other complementary ions such as Ca^{2+}, Mg^{2+} and NO_3^- , and therefore, further investigation requires altered transport and compartmentation mechanism of these nutrients under salinity stress. In plants, predominantly three distinct but complementary mechanisms operate cooperatively that selectively inhibit the accumulation of Na^+ in the cytoplasm following one or other processes, i.e. checking of Na^+ influx, promotion of active Na^+ efflux and sequestration of Na^+ in the vacuole, which will be discussed categorically in this compilation. But before that we need to understand various soil-related factors affecting availability of nutrients under salt stress.

14.2 Soil-Driven Factors Affecting Nutrient Availability Under Salt Stress

14.2.1 Salinity: Origin and Extent

Salinity is predominant in two major forms over the land surface, (1) dry land salinity and (2) irrigation salinity, and arid and semiarid climatic regions throughout the world are suffering due to salinity in one form or another. The dry land salinity is often detected as primary or secondary salting, either occurring naturally (naturally occurring saline wet and dry lands including salt lakes, salt pans, salt marshes and salt flats) or via secondary salting that is induced by human activities such as agriculture (Fig. 14.1). Secondary salinity is majorly caused by anthropogenic activities, while practising land development and agriculture may play some role (Queensland Government 1995–2017), and the common forms are:

- Irrigation: prevalent in irrigated agricultural lands, due to excessive irrigation (results into rising groundwater tables) or the application of poor-quality water.
- Dry land: prevalent in rainfed or nonirrigated landscapes, generally as a result of deforestation and land-use changes. Irrigation salinity often resembles dry land salinity, except that inclined level of groundwater that also resulted in deposition of salt layers in the plant root zone or on the soil surface.
- Sea water intrusion: In coastal aquifer systems, it is commonly found that fresh groundwater is gradually replaced by sea water.

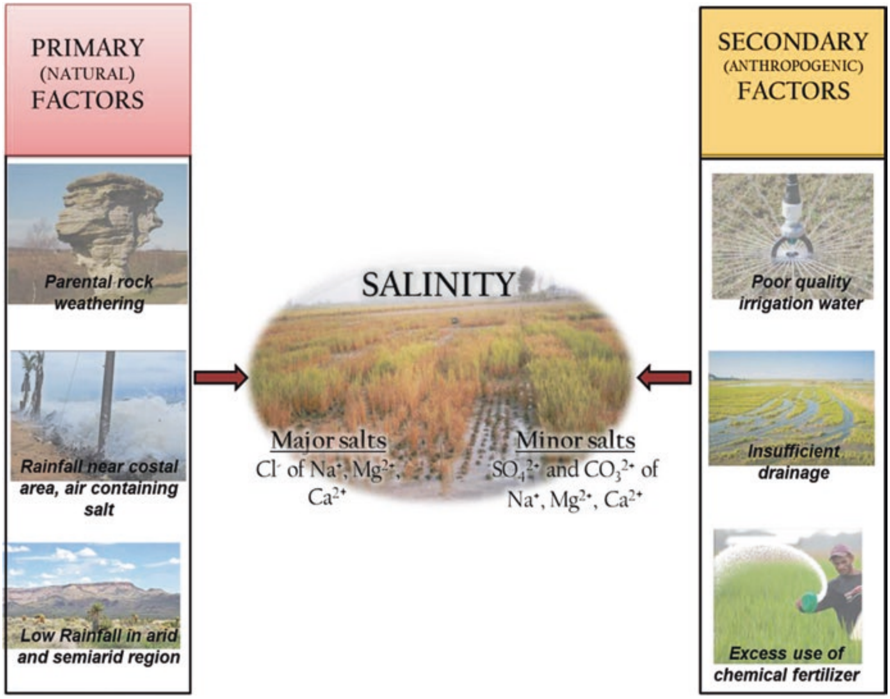

Fig. 14.1 Causes of different types of salinity resulting in ionic imbalance in soil

- Point source: originated from the high concentration of diluted salt in effluent either released from intensive agriculture loaded with pesticide/chemical residues or from polluted wastewater stream from industries.

Over the years, several estimations have been published regarding the extent of salinity. Oldeman et al. (1991) reported that the total area affected by waterlogging was over 10 m ha and that affected by salinity was over 76 m ha. They counted both irrigated and rainfed areas. Dregne et al. (1991) published that about 43 m ha of irrigated land in dry lands was affected by several forms of degradation, including waterlogging, salinization and sodicity. Umali (1993) estimated that 1–1.5 m ha of lands were lost to salinization every year. Further it had been reported that nearly 12 m ha of irrigated land may have phased out from production due to salinization (Nelson and Maredia 2001). An approximate area of 7 m ha of land is estimated to be under saline soil in India (Patel et al. 2011). These lands are classified in Table 14.1.

Table 14.1 Classification of salt-affected soil

	USDA classification			SSSA classification	
Nature of soil	EC_e (dSm^{-1})	pH	ESP	EC_e (dSm^{-1})	SAR
Normal	<4.0	<8.5	<15	<2	<13
Saline	>4.0	<8.5	<15	>2	<13
Sodic	Variable	>8.5	>15	Variable	>13
Saline-sodic	>4.0	>8.5	Variable	<2	>13

Source: *Handbook of Agriculture* (2011)

Table 14.2 Impact of soil degradation on Indian agriculture

Crop	Percent loss
Paddy	2.7–4.7%
Wheat	3.9–6.4%
Barley	4.5–7.0%
Groundnut	2.8–4.4%
Gram	5.6–7.8%
Rapeseed and mustard	5.8–8.5%
Jowar	5.7–7.6%
Bajra	6.8–8.4%
Cotton	5.3–6.9%
Maize	3.2–4.9%
Sugar cane	4.5–7.9%
All other crops	4.0–6.3%
Total	4.0–6.3%

Source: *The Cost of Inaction*: *Valuing the Economy-Wide Cost of Environmental Degradation in India* (Brandon and Homman 1995)

14.2.2 Salinity Impacts on Crop Production

Agriculture is one of prime importance as far as salinity hazard is concerned. Crops may differ in their tolerance to salinity, and some of them are extremely sensitive, while few perform better even after crossing the threshold of marginal salinity and emerge as tolerant crops in terms of salinity stress. Even varietal differences are also prominent in major field crops. A report published from World Bank showed the degree of loss and major impacts due to salinity or other forms of soil degradation as a whole (Table 14.2; Fig. 14.2).

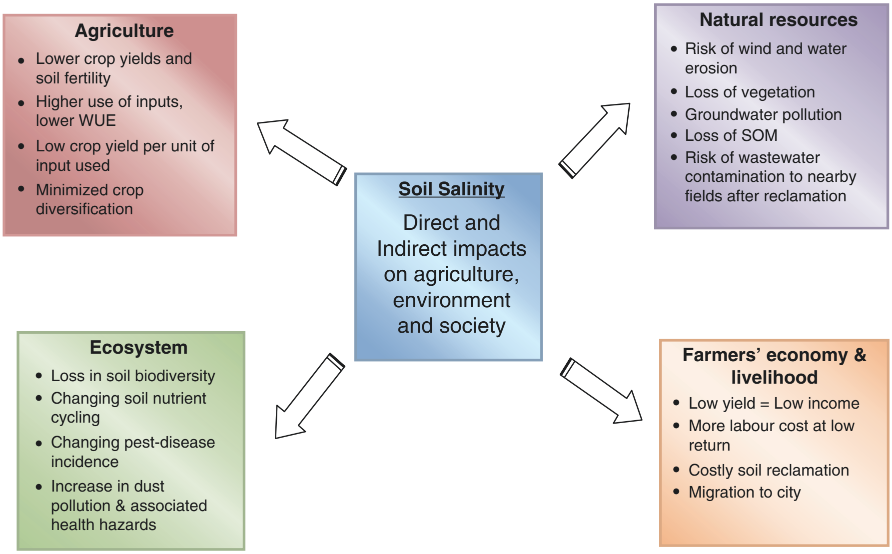

Fig. 14.2 The most promising impacts of soil salinity (FAO 2017)

14.2.3 Salinity Impacts on Nutrient Mobility in Soil and Plants

Besides the crop yield perspective, soil salinity has its own demerits creating problems like nutrient loss, nutrient imbalance, poor soil structure and health, and soil degradation. Dry land salinity is often considered as a major soil degradation issue, including soil erosion. Salinity is often associated with prolonged wetness, sparse vegetation and lack of surface cover and therefore increases the vulnerability of soils to erosion. Salt concentration in the soil solution (salinity) which governs the osmotic potential and the concentration of sodium on the exchange complex sites (sodicity) further determines soil structural stability. Thus, salinity slowly turns into sodicity. The major soluble salts in soils are the cations like Na^+ (sodium), Ca^{2+} (calcium), Mg^{2+} (magnesium) and K^+ (potassium) and the anions like Cl^- (chloride), SO_4^{2-} (sulphate), HCO_3^- (bicarbonate), CO_3^{2-} (carbonate) and NO_3^- (nitrate) (Shi et al. 2005). These are the basic ions that dominate in the exchange sites under salinity and thus compromise the places of other essential nutrients like PO_4^{3-} (phosphate) and micronutrients (Zn, Fe, Mn, Cu). This imbalance of nutrients created in soil is often measured by nutrient concentration or uptake by plants comparing the plants grown under normal and saline conditions. Similar occurrence was reported by Bhaduri et al. (2016) where P uptake of eight groundnut cultivars were studied and observed that the P uptake of groundnut cultivars is affected at irrigation salinity level of 6.0 EC_{iw}. Salinity stress lowered down the N content in *Brassica* leaves as well as seed protein content; moreover the reduced accumulation of micronutrients (Fe, Mn, Zn) was also noticed in the leaf, stem and root at flowering and post-flowering stages (Chakraborty et al. 2016b).

Soil microorganisms, an integral component of soil ecosystem, are largely involved in an array of important soil nutrient cycling processes. Their roles in nitrification, ammonification, nitrogen fixation, P mineralization, S oxidation, decomposition of soil organic matter and transformation of all primary and secondary nutrients (Amato and Ladd 1994) are already established. Microbes also act in formation of humic substances which makes stable forms of organic C and contribute in C sequestration in soils. The high concentration of soluble salts affects the microbes by increasing the osmotic potential (more negative) of the soil water, promotes exosmosis and dehydrates the microbial cell. Thus, it makes difficult for microbes to survive and perform their basic functions in a saline soil. Even if they can survive under such stressful situation that needs more investment of energy for producing osmolytes. Till date, only few halophytic microbes and some endophytes are reported to tolerate such extreme saline conditions. Moreover, soil microbial community structure also differs significantly since fungi are more salt sensitive over bacteria, and thus bacteria/fungi ratio can be increased under saline soil environment (Wichern et al. 2006; Yan et al. 2015). All these phenomena either singly or collectively influence the soil nutrient availability.

14.3 Uptake of Regulatory Ions in Plant Cells: An Interplay of Nutrient Balance/Imbalance

Salinity is a much complex phenomenon rather than a simple escalation in the concentrations of sodium and chloride ions inside the plant tissue (Nouri et al. 2017). Apart from Na^+ and Cl^-, number of other cations and anions, viz. calcium, carbonates and sulphates, may be present in disproportionate amounts and play crucial role in negatively affecting plant growth (Gorham 1992). Simultaneously, certain nutrients (particularly potassium, nitrogen and phosphorus) may be available or present in such low amounts under saline condition that they might hamper proper growth (Chakraborty et al. 2016c).

Saline conditions affect plant growth and metabolism in many different ways. These harmful effects are generally associated with (1) reduced osmotic potential of the soil solution in plants (water stress), (2) nutritional imbalance, (3) effect exerted by a specific salt (salt stress) or (4) a combination of all of these factors (Ashraf and Foolad 2007; HanumanthaRao et al. 2016). These factors act in an adverse way affecting growth and development in plants at both physiological and biochemical levels (Munns 2002; Munns and Tester 2008) and also at the molecular level (Tester and Davenport 2003). Tolerance to saline conditions involves a myriad number of physiological processes manifested in numerous levels of organization, viz. alterations in gross morphology, tissue partitioning and coordinated control of transport, biological change for maintenance of protein structure and regulated transcriptome level changes (Tester and Davenport 2003).

14.3.1 Scenario of K^+ vs Na^+ and K^+/Na^+ Homeostasis Under Salt Stress

Sodium, an integral constituent of our Earth's crust, is naturally present in all soil types. At lower concentration Na^+ helps in supporting growth and development for some plants, but at higher concentration in soil or other growing medium, it eventually turns out to be toxic to even glycophytes (Flowers and Colmer 2008). Both Na^+ and K^+ share high similarity in ionic as well as its chemical and structural properties, but unlike Na^+, K^+ are integral part of plant's life and play essential role in growth and development (Schachtman and Liu 1999). Many core physiological processes, primarily dependent on K^+, show impairment due to hindrances in specific transport and interactions of K^+ with enzymes and membrane proteins (Britto and Kronzucker 2008). This may be manifested as transient maintenance of membrane potential for stomatal movement and development of pollen tube in plants (Dietrich et al. 2001). Under saline condition, due to prolonged exposure to salt stress, plants often exhibit K^+ deficiency symptoms majorly because of reduced uptake by the root tissue and/or lesser K^+ retention in different plant parts coupled with a concomitant accumulation of tissue Na^+ concentration (Munns et al. 2002). Under salt stress, plants with hindered growth and metabolism are observed due to the skewed K^+/Na^+ ratio in metabolically active plant tissues (Shabala and Cuin 2007; Degl'Innocenti et al. 2009). Because of such ionic imbalances, hindrances in various physiological and biochemical processes are observed in plants.

Under high external Na^+ concentrations, Na^+ enters through K^+ pathway altering the ion ratios in plants. The similarity of the ionic radii of the hydrated molecule of Na^+ and K^+ renders the capability of discrimination between them much difficult and hence forms the basis of Na^+ toxicity. Cellular K^+ concentrations in the range of 100–150 mM are essential for in vitro protein biosynthesis. Moreover, at higher concentrations, Na^+ competes for K^+ sites and inhibits the whole process when Na^+ concentrations is >100 mM (Cheeseman 2013). The similar level of sensitivity of cytosolic enzymes of halophytes and glycophytes towards saline conditions hinders the adaption of halophytes to high salt concentration (Flowers et al. 2014). Maintenance of low cytosolic Na^+ concentrations and a high cytosolic K^+/Na^+ ratio is a key strategy adapted by plants to respond to elevated external Na^+ concentrations (Blumwald et al. 2000). The approach towards such maintenance involves extrusion of Na^+ or its compartmentalization mainly in the vacuoles for metabolism (Zhu 2003) and is critical for the detoxification of excess Na^+ present in cytosol and the osmotic adjustment necessary to endure salt stress (Blumwald et al. 2000; Chakraborty et al. 2016d).

14.3.2 Regulation of Tissue Na^+ Concentrations

14.3.2.1 Sodium Uptake

On exposure to salt stress, maintenance of low concentrations of Na^+ and high concentrations of K^+ in the cytosol becomes crucial and is achieved by controlled expression and activity of K^+ and Na^+ transporters (Shabala et al. 2015). Na^+ enters the plant cells passively through the high-affinity K^+ transporter HKT1 (Rus et al. 2001; Maser et al. 2002) and non-selective cation channels (NSCCs). Due to non-selectivity of a few transporters and/or ion channels, under highly saline conditions, Na^+ ions compete with K^+ ions for uptake and enter inside the plant through normal rhizospheric nutrient uptake process. At transcriptional level, these K^+/Na^+ transporter genes are either up- or downregulated as a response to salt stress (Chakraborty et al. 2016e). It has been reported that the transcript level of *Arabidopsis* root K^+ transporter *AtKC1* increases under salt stress (Pilot et al. 2003). As reported by Zhu (2003), upregulation in the expression level of *KMT1* (a AKT/KAT family member) and various *HAK/KUP* (high-affinity K^+ transporter/K^+ uptake transporter)-type genes was observed, whereas for *MKT1* (another *AKT/KAT* family member), the expression level was found to be downregulated for common ice plant.

14.3.2.2 Sodium Efflux

The primary mechanism of Na^+ extrusion in case of plants is mediated by energy-driven active pumping out of Na^+ by plasma membrane-bound Na^+/H^+ transporter and H^+-ATPases (Zhu 2001). The H^+-ATPase acts to pump H^+ out of the cell using the energy of ATP hydrolysis, thus generating an electrochemical proton gradient. The proton-motive force thus generated is further required for the Na^+/H^+ antiporter operation as the inward movement of H^+ along with the electrochemical gradient is coupled to the outward exclusion of Na^+ against the electrochemical gradient. Confirmation of the existence of such biochemical mechanism has been documented for various plant species (Blumwald et al. 2000). Identification of a putative Na^+/H^+ antiporter with substantial similarity in sequence with plasma membrane Na^+/H^+ antiporters from bacteria and fungi has further strengthened the views. The *SOS1* (salt overly sensitive 1) locus encoding a putative Na^+/H^+ antiporter having considerable sequence similarity to plasma membrane Na^+/H^+ antiporters from bacterial and fungal species has been identified in *Arabidopsis* (Shi et al. 2000), rice (Martinez-Atienza et al. 2007), wheat (Yang et al. 2009) and in *Brassica* (Chakraborty et al. 2012a).

14.3.2.3 Vacuolar Sodium Compartmentation

It has been observed that both halophytes and glycophytes regardless of the high influx of Na^+ maintain the cytosolic concentration of the ion at non-toxic levels (Blumwald et al. 2000). The compartmentalization of Na^+ into vacuoles has been found to be the primary mechanism of evading the harmful effects Na^+ exerts in the cytosol. Additionally, the vacuolar compartmentalization of Na^+ (and Cl^-) allows the usage of NaCl as an osmoticum thereby contributing in maintenance of an osmotic potential for the process of water uptake into cells (Blumwald et al. 2000). Tonoplast-bound vacuolar Na^+/H^+ antiporters (NHX family transporters) play crucial role in Na^+ compartmentalization inside the cell (Yokoi et al. 2002). Identification and characterization of several plant transporters have been made possible by detection of the higher degree of homology between several plant and yeast genes, and the detailed genetic information is available in the public domain (Halfter et al. 2000; Ji et al. 2013). Evidences suggest that Na^+ detoxification mechanisms employed in yeast cells may be found to be quite similar to that existing in plant cells. This similarity mostly holds true for the role played by the Ca^{2+}-dependent signal transduction mechanism which becomes operational under salinity stress (Halfter et al. 2000). Putative Na^+/H^+ antiporters (both SOS1 and NHX family) from both organisms are also similar (Apse et al. 1999; Fukuda et al. 1999).

14.3.3 Interaction Between Na^+ and Ca^{2+}

An important inorganic nutrient, calcium, plays a vital role in salt detoxification, in addition to its well-known metabolic and structural functions (Jin et al. 2007). This response stems from the fact that increasing Na^+ concentrations may not only reduce Ca^{2+} availability but may also displace Ca^{2+} from its extracellular binding sites within the plant organs and further disrupt Ca^{2+} acquisition (Hadi and Karimi 2012). The interaction between Na^+ and Ca^{2+} in salt-stressed plants has been the focus of several research agendas over the years (Cramer 2002; Nedjimi and Daoud 2009). It has been advocated that Na^+ tolerance of plants is determined to a larger extent by interactions of Ca^{2+} and Na^+ ions (Buschmann et al. 2000). It is reported that high NaCl induces calcium deficiencies in different plants such as *Vigna unguiculata* (Murillo-Amador et al. 2006) and tomato (Tuna et al. 2007). Allen et al. (1995) reported that Na^+ influx on durum wheat cells can also be inhibited by calcium. According to Jin et al. (2007), saline conditions restricted Ca^{2+} uptake by the roots of *Aloe vera* plants and its subsequent transport to shoots resulting in a marked decrease in Ca^{2+} contents of all plant parts. It was further reported that in plants under salt stress, the Ca^{2+} contents of the leaves and stems show a noticeable decrease; salt-tolerant genotypes were found to exhibit three times higher Ca^{2+} concentrations as compared to salt-sensitive ones.

High Na^+ concentration in the root zone was found to inhibit Ca^{2+} uptake and its transport resulting in lower Ca^{2+}/Na^+ ratios in salt-stressed plants (Hadi et al. 2008). Additionally, Jin et al. (2007) showed that salt-tolerant genotypes of *Aloe vera* maintained a significantly low Na^+/Ca^{2+} ratio and experienced least membrane damage. The rapid Na^+ uptake process across the plasma membrane in excess salt condition diminishes the binding capability of Ca^{2+} to the plasma membrane thus inhibiting its influx. High Na^+ concentrations can displace Ca^{2+} in membrane thus disrupting the integrity of it (Janicka-Russak and Kłobus 2007). Hasegawa et al. (2000) in their report indicated that the increase in intercellular Ca^{2+} content could cause a decline in Na^+ influx and in turn increase the K^+ selectivity for absorption thus alleviating the damaging effects of salinity stress. They also pointed out that under salinity stress, Na^+ can compete with Ca^{2+} by entering the cell through the same channels. The excess intercellular sodium can then displace the Ca^{2+} in the membranes causing membrane damage. Membrane-bound catalase activity could also be inhibited by excess Na^+ which can be reversed by excess Ca^{2+} (Arbona et al. 2003). It has been proposed that Ca^{2+} plays a central role in plants exposed to NaCl salinity because of its active participation in reducing Na^+ absorption and increasing potassium (K^+) and Ca^{2+} uptake, resulting in an increase in plant growth (Caines and Shennan 1999). Additionally, Ca^{2+} may compete with Na^+ for membrane-binding sites thereby shielding the cell membrane from the unfavourable saline conditions (Shabala et al. 2006).

The $[Ca^{2+}]_{ext}$ augments salt tolerance by eliciting a transient increase in $[Ca^{2+}]_{ext}$ either from a peripheral or an internal source (Knight et al. 1997). Experiments conducted on yeast have generated preliminary views of Ca^{2+}-mediated activation of signalling pathways for regulation of ionic homeostasis and tolerance mechanisms in response to salt stress conditions. A suggestive model for salt-induced Ca^{2+} signalling and activated SOS pathway includes components of the SOS pathway; the SOS3 or other upstream elements might become connected with the osmotically responsive channel triggering Ca^{2+} influx which might possibly initiate signalling through the pathway (Chakraborty et al. 2016e). Reports suggests that salt-induced $[Ca^{2+}]_{ext}$ transient as well as the new $[Ca^{2+}]_{ext}$ steady state may be influenced by the ECA and ACA Ca^{2+}-ATPases as well as the CAX1 and CAX2 transporters, the orthologs of VCX1P (Sze et al. 2000). Ca^{2+} plays two vital roles in conferring tolerance towards salinity, the fundamental signalling function leading to adaptation during salt stress conditions and a direct inhibitory effect on the entry of Na^+ ions.

14.3.4 Transport and Xylem Loading

Na^+ transport across the root and into the xylem occurs both symplastically and apoplastically from the epidermis to the xylem (Maathuis et al. 2014). Na^+ export to the xylem is supposed to be an active process, given that the electric membrane potential of xylem parenchyma has been found to be negative. In *Arabidopsis*, under the conditions of salinity, xylem loading of Na^+ was found to be mediated by SOS1 (salt overly sensitive1), while its unloading, on the other hand, was found to be a passive process, involving transportation through the Na^+-permeable channels (Apse and Blumwald 2007). High-affinity K^+ transporters or HKTs, classified in class I and class II types, were one of the most studied Na^+-permeable transporters in plants (Horie et al. 2009). These HKT transporters, often located in the xylem parenchyma and root epidermal cells of many plants, exhibit a crucial role in adapting the plant to saline conditions for both mono- and dicotyledonous species (Møller et al. 2009; Munns et al. 2012). The class I HKT transporters showing specificity for mostly Na^+ ions are characterized as low-affinity transporters (Munns and Tester 2008). Among the different subtypes of HKT1 transporter, a few are reported to be located in the plasma membrane of root stele cells, particularly in the xylem parenchyma cells (XPC), where their main function is to regain the Na^+ ion from the xylem sap thereby avoiding transport and accumulation of toxic Na^+ in the above ground plant parts and preventing damage to the more sensitive and photosynthetically active tissues (Ren et al. 2005).

14.4 Mechanisms of Nutrient Homeostasis: A Balancing Approach of Plants Facing Salt Stress

Physiological studies carried out in many crops during salt stress at vegetative stage indicated that stress tolerance trait inversely correlates with shoot Na^+ concentration and Na^+/K^+ ratio (Ashraf 2004; Negrão et al. 2011). Different mechanisms associated with salt tolerance in crop plants include (1) maintenance of a more negative membrane potential, (2) intrinsically higher H^+-ATPase activity, (3) extrusion of Na^+ from the cytosol to the external medium, (4) maintenance of mineral nutrient homeostasis, particularly, higher selectivity to K^+ and Ca^{2+} over Na^+, (5) scavenging of ROS, (6) accumulation of compatible solutes for osmotic adjustment, etc. At the physiological level, salt tolerance and ion homeostasis are mostly governed by three major strategies in crop plants: (I) Na^+ exclusion, (II) K^+ retention and (III) tissue tolerance/Na^+ sequestration (Munns and Tester 2008).

14.4.1 Electrophysiological Basis of Salt Tolerance: Role of Transporter/Pumps/Ion Channels

Plant salinity stress signalling is a complex phenomenon involving the interplay of many biomolecules ranging from receptor molecules, ion fluxes that serve as signals, transcription factors, hormones, reactive oxygen species (ROS) and numerous downstream proteins. In the cyanobacterium, *Synechocystis* sp., Marin et al. (2003) identified sensory histidine kinases, namely, HIK16, HIK33, HIK34 and HIK41, involved in the perception and transduction of salt stress. In plants, there is less clarity about the proteins that perceive salt stress. Salt overly sensitive (*SOS*) genes (*SOS1-SOS4*), first identified in *Arabidopsis thaliana* through positional cloning, are potential candidates for detecting elevated Na^+ concentrations in intracellular and extracellular sites. The AtSOS1 protein is a putative plasma membrane Na^+/H^+ antiporter that regulates plant Na^+ homeostasis by extrusion and is aided in its function by two other proteins SOS2 and SOS3 (Qiu et al. 2002; Zhu 2003). SOS-mediated salt stress signalling is represented in Fig. 14.3. The *sos1*, *sos2* and *sos3* mutants show salt

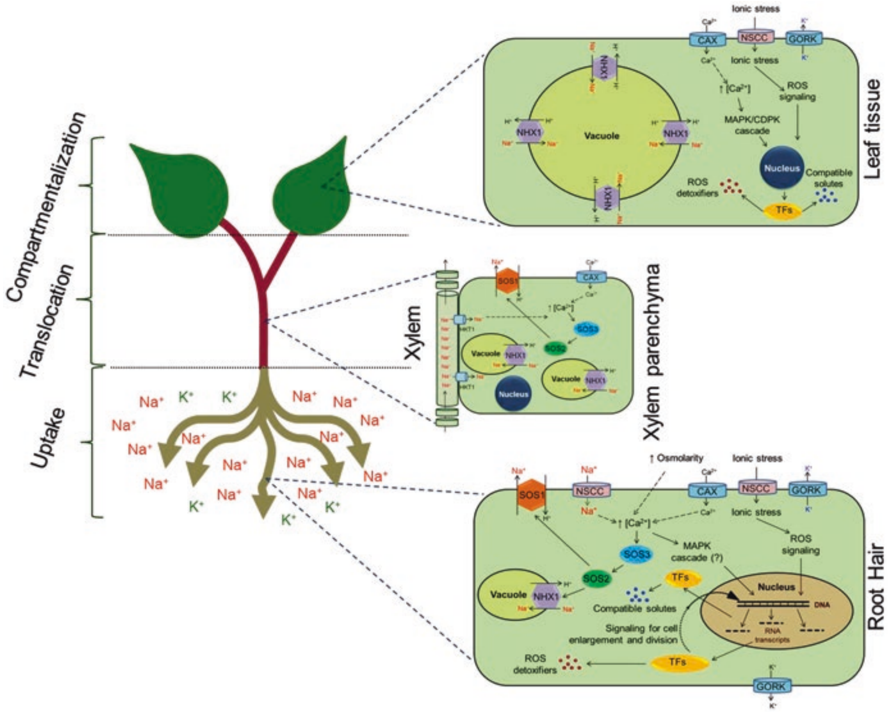

Fig. 14.3 A coordinated network of Na^+ and K^+ transport in different plant parts under salinity stress

sensitive phenotype, and their genetic analysis has helped to improve our understanding of the mechanism of salt stress tolerance in plants (Zhu et al. 1998). Yeast mutants lacking endogenous Na^+ transporters were used to investigate the role of the three SOS proteins in salt-stress response pathway (Quintero et al. 2002). Perception of salt stress is followed by subtle changes in Ca^{2+} concentration in cytosol of root cells that triggers the SOS pathway (Guo et al. 2004; Chinnusamy et al. 2005). SOS3 is a myristoylated Ca^{2+}-binding protein that recruits SOS2 serine-threonine protein kinase to the plasma membrane after binding of Ca^{2+} (Ishitani et al. 2000; Halfter et al. 2000). An alternative regulator of SOS2 activity, SOS3-like calcium-binding protein 8 (SCaBP8, a.k.a. calcineurin B-like CBL10), has been shown to function primarily in the shoots of *Arabidopsis*, while *SOS3* expresses predominantly in roots (Quan et al. 2007). SOS2-mediated phosphorylation of SCaBP8 or SOS3-like proteins increases their stability (Lin et al. 2009). The SOS3-SOS2 or SCaBP8-SOS2 complex then recruits SOS2 to plasma membrane to activate downstream *SOS1*, which functions to extrude excess Na^+ from the cytosol (Shi et al. 2000; Qiu et al. 2002; Quintero et al. 2002, 2011; Quan et al. 2007). SOS4 and SOS5 also play important roles in salt stress tolerance. While *SOS4* encodes a pyridoxal kinase that is involved in regulation of Na^+ and K^+ homeostasis (Shi et al. 2002), *SOS5* aids in the maintenance of normal cell expansion during stress (Shi et al. 2003).

Other Na^+ transporters functioning in salinity tolerance include those involved in intracellular compartmentalization of Na^+ into vacuoles, older leaves or leaf sheath, extrusion outside the cell and recirculation of Na^+ out of the shoots to be stored elsewhere, for example, in roots or stem cell vacuoles. Vacuolar Na^+ sequestration is one of the most energetically efficient mechanisms by which plants achieve turgor maintenance and cell expansion in saline conditions. The NHX-type intracellular Na^+/H^+ exchangers that mediate this process are driven by the differential proton (H^+) gradient generated by vacuolar H^+-translocating enzymes such as H^+-ATPase and H^+-PPase. Plant NHX family can be divided into two groups, class I and class II, based on protein sequence and subcellular localization (Rodriguez-Rosales et al. 2009; Pardo et al. 2006). The class I NHX proteins are located on the tonoplast, where they function as (Na^+, K^+)/H^+ antiporters (Venema et al. 2002), while the class II NHX proteins are located in endosomal vesicles of plants (Bassil et al. 2011). These proteins maintain K^+ homeostasis and function in aiding normal plant growth and development as well as tolerance to salt stress (Pardo et al. 2006). The *AtNHX1* gene, the first plant member of the NHX subfamily of intracellular Na^+/H^+ antiporters from *Arabidopsis thaliana*, was identified based on its homology to animal plasma membrane Na^+/H^+ antiporters of the NHE family and the yeast *ScNHX1* gene (Gaxiola et al. 1999). Overexpression of *AtNHX1* in other plant systems led to improved salt stress tolerance (Zhang and Blumwald 2001; Zhang et al. 2001). A different model for the role of NHX transporters has been proposed by Jiang et al. (2010), which states that the NHX proteins function mainly to prevent toxic Na^+/K^+ ratios in the cytosol and for maintaining osmotic balance which is achieved by the vacuolar compartmentalization of Na^+ and, in some cases, of other cations as well. A wheat NHX antiporter, *TaNHX2*, having significant sequence homology to *NHX* sodium exchangers as reported from *Arabidopsis*, was found to suppress the salt sensitivity of a yeast mutant strain by improving its K^+ content when faced the salt stress (Xu et al. 2013). Here an attempt had been made to compile reported transporters/ion channels/pumps associated with movement of Na^+ and K^+ in plants (Table 14.3).

14.4.2 Transcription Factor (TFs) Involved in Salinity Stress Tolerance and Ion Homeostasis

In order to impart enhanced salt tolerance, it is essential to develop a basic understanding of biochemical, physiological and gene regulatory networks of stress response pathways. Transcription factors (TFs) play a critical role in signal transduction network starting from the perception of stress signal to the expression of stress-responsive genes. Unlike the structural genes, TFs tend to control several complex pathways (master regulator) making them one of the ideal candidates for pathway manipulation. Several TFs (OsRAB1, MYC/MYB, OsNAC/SNAC, etc.) have been identified which are differentially expressed during adaptation to salt stress; interestingly, many of these TFs are also differentially expressed during other

Table 14.3 A glimpse at the probable transporters playing a role in salinity tolerance with inputs from Almeida et al. (2013, 2017), Maathuis (2006), Kumar and Mosa (2015) and Shabala and Pottosin (2010)

Name of transporter	*In-planta* expression	Physiological role	References
OsHKT1;1	Roots: Similar as *OsHKT2;1*. Leaves: bulliform cells and vascular tissues	Control of Na^+ concentration in phloem sap	Garciadeblas et al. (2003), Jabnoune et al. (2009) and Wang et al. (2015)
OsHKT1;2	Leaves, though expression does not change under stress	Codes for a pseudogene	Wu et al. (2009) and Phuc et al. (2016)
OsHKT1;3	Roots: cortex and vascular tissues in the stele. Leaves: bulliform cells and vascular tissues, mesophyll cells	Mediates both inward and outward Na^+ current	Wu et al. (2009) and Almeida et al. (2013)
OsHKT1;4	Leaf sheaths	Control sheath to blade Na^+ transfer	Cotsaftis et al. (2012)
OsHKT1;5	Roots and shoots: xylem parenchyma	Control root to shoot Na^+ transfer	Ren et al. (2005)
TaHKT1;4	Root, leaf sheath, leaf blade	Unloading of Na^+ from xylem into xylem parenchyma cell	Huang et al. (2006)
TaHKT1;5	Roots	Unloading of Na^+ from xylem into xylem parenchyma cell	Byrt et al. (2007)
AtHKT1;1	Roots: xylem parenchyma, phloem Shoots: phloem	Loading of excess Na^+ from shoot into phloem Unloading of Na^+ from xylem into xylem parenchyma cells	Møller et al. (2009) and Sunarpi et al. (2005)
OsHKT2;1	Roots: epidermis, exodermis, cortex differentiated into aerenchyma, stele (mainly pholem). Leaves: bulliform cells, xylem, phloem, mesophyll cells	Uptake of nutritional Na^+ from external medium	Horie et al. (2007)
OsHKT2;2	Roots only	Na^+/K^+ symporter; cotransports both Na^+ and K^+ under low K^+ concentration	Yao et al. (2010)
OsHKT2;2/1	Roots	Cotransport of both Na^+ and K^+ under salt stress	Oomen et al. (2012)
OsHKT2;3	Shoots, marginal expression in roots	Cotransport of both Na^+ and K^+ under salt stress	Horie et al. (2011)
OsHKT2;4	Roots, leaf sheaths, spikelets, base of stems	K^+ transporter/channel	Lan et al. (2010)
TaHKT2;1	Roots: cortical and stele. Leaves: vasculature tissue of mesophyll	Uptake of Na^+ from the external media	Laurie et al. (2002)

(continued)

Table 14.3 (continued)

Name of transporter	*In-planta* expression	Physiological role	References
HvHKT2;1	Roots: cortex. Leaves: blade and sheath	K^+ absorption in root at very low K^+ concentrations	Haro et al. (2005) and Mian et al. (2011)
OsAKT1	Coleoptile and roots of rice seedlings	Inward-rectifying K^+ channel regulated by extracellular Ca^{2+} and protons	Fuchs et al. (2005)
AtAKT1	Root cortex, endodermis, epidermis, hair, leaf mesophyll	Low-affinity K^+ uptake	Pilot et al. (2003)
AtAKT2/3	Xylem, phloem, guard cell, leaf mesophyll	Weakly inward rectifying K^+ channel	Pilot et al. (2003)
OsMKT1	Roots	Inward-rectifying channel	Su et al. (2001)
OsKAT1	Internodes	Inward-rectifying channel	Obata et al. (2007)
AtKAT1	Guard cell	Inward-rectifying channel	Szyroki et al. (2001)
AtSKOR	Root pericycle, stellar parenchyma	Stelar K^+ outward rectifier, virtually impermeable to Na^+	Pilot et al. (2003) and Qi and Spadling (2004)
OsNHX1	Roots: stela, emerging parts of lateral roots Shoots: basel part of seedling shoot, vascular bundle, flag leaf sheaths, panicles, guard cells, trichome	Vacuolar Na^+/H^+ antiporter	Fukuda et al. (2004)
OsNHX2	Shoots: flag leaf sheaths, panicles	Vacuolar Na^+/H^+ antiporter	Fukuda et al. (2011)
OsNHX3	Shoots: flag leaf sheaths, panicles	Vacuolar Na^+/H^+ antiporter	Fukuda et al. (2011)
OsNHX4	N/A	Vacuolar Na^+/H^+ antiporter	Fukuda et al. (2011)
OsNHX5	Roots: stela, emerging parts of lateral roots, root tip. Shoots: basel part of seedling shoot, vascular bundle, flag leaf sheaths, panicles, pollen grain	Endosomal K^+/H^+ antiporter	Bassil et al. (2012)
AtNHX1	Roots: vascular tissues. Shoots: floral and vascular tissues, guard cells, trichome	Vacuolar Na^+/H^+ antiporter	Rodríguez-Rosales et al. (2009)
AtNHX2	Root shoots: high in guard cells	Vacuolar Na^+/H^+ antiporter	Yokoi et al. (2002)
AtNHX3	Mainly in roots	Vacuolar Na^+/H^+ antiporter	Yokoi et al. (2002)
AtNHX4	Shoots: mainly in mature pollen and seeds	Vacuolar Na^+/H^+ antiporter	Yokoi et al. (2002)

(continued)

Table 14.3 (continued)

Name of transporter	*In-planta* expression	Physiological role	References
AtNHX5	Root shoots: high in guard cells	Endosomal K^+/H^+ antiporter	Bassil et al. (2011)
AtNHX6	Root shoots: high in guard cells	Endosomal K^+/H^+ antiporter	Bassil et al. (2011)
AtNHX7/ SOS1	Roots: epidermal cells (particularly root tip), parenchyma cells lining the vasculature shoots	Plasma membrane Na^+/H^+ transporter	Kronzucker and Britto (2011)
TaNHX2	Root	Endomembrane bound K^+/H^+ antiporter	Xu et al. (2013)
OsCAX4	Embryo, roots, leaf sheaths, shoots and nodes	Vacuolar cation exchanger	Kamiya et al. (2005)
AtCAX1	N/A	Cation exchanger	Cheng et al. (2003)

stresses. In particular, there are many common TFs that control gene expression both during salt and drought stress. A comprehensive database of rice TFs involved in adaptation of salt and drought is available at Rice Stress-Responsive Transcription Factor Database (RiceSRTFDB; http://www.nipgr.res.in/RiceSRTFDB.html) (Priya and Jain 2013). A recent study on transcriptome analysis of common bean (*Phaseolus vulgaris* L.) under salt stress has reported differential expression of 59 different families of TFs among which 10 TF families, viz. *AP2-EREBP*, *bHLH*, *PHD*, *HB*, *(R1)R2R3_Myb*, *WRKY_Zn*, *NAC*, *bZIP*, *C3H-TypeI* and *Myb_related*, were most abundant (Hiz et al. 2014). A comparison of transcriptome of salt-sensitive (Hua 30) and salt-tolerant (Hua 11) barley varieties under salt stress has also shown differential expression of several transcription factors belonging to different families, such as TIFY (earlier known as ZIM), WRKY, zinc finger, MYB, bHLH, CBF, NAC, bZIP, AP2, whirly, HD-ZIP, etc. Two interesting observations of this study were that (i) the number of differentially expressed genes was more in shoots as compared to roots and (ii), compared to control, more number of genes were found to be upregulated in response to salt stress than downregulated (Gao et al. 2013). Cloning and validation of such salt stress-responsive TFs is a step in the right direction for improvement of salinity tolerance in crops. For example, stress-specific *NAC1* (*SNAC1*) cloned from rice landrace Pokkali (Hu et al. 2006) was found to confer salt stress tolerance in rice by working downstream to ABA-induced salt and drought tolerance pathway (Khong et al. 2008). Similarly, OsMYB48-1 conferred tolerance to salt stress along with drought in rice (Xiong et al. 2014). On the other hand, cold-induced MYB 1 (CMYB1) which is involved in cold tolerance and circadian rhythm maintenance in rice is negatively correlated with salt stress tolerance. Many of these cloned TFs are trans-acting, i.e. they can impart salt tolerance in different (non-native) backgrounds. For example, OsDREB2A, a transcription factor of AP2/ERF family in rice is capable of imparting salt tolerance in transgenic soybean by accumulation of higher level of osmolytes (Zhang et al. 2013). Some of the other such transacting TFs are OsMYB3R-2 (Dai et al. 2007), HvCBF4 (Oh et al. 2007), DREB1A (Oh et al. 2005), NAC (Tran et al. 2004), etc. If regulated properly in the transgenic background, these trans-acting TFs can work to regulate pathways in any of the desired crops and thus be ideal candidates for engineering salt stress tolerance in crop plants.

14.4.3 Post-transcription Gene Regulation and Adaption to Salt Stress

Apart from the transcription factors, which play a role as master switches to control and coordinate transcription of several genes, a plethora of genes are also controlled post-transcriptionally under salinity stress. This post-transcriptional regulation is achieved through a group of salt-responsive microRNAs (miRNAs), a class of small non-coding RNAs of ~21 nucleotide length, which exerts an additional level of control over plant gene expression under stress. In fact, miRNAs are now considered as one of the major players in gene regulation which downregulate expression of their target genes by mRNA cleavage or translation-arrest mechanisms based on the perfect or near-perfect complementary pairing, respectively (Ambros 2004). A plethora of miRNAs have been demonstrated to play a role in several stress tolerance pathways; some of them are found to be involved in multiple stresses and across species (Dugas and Bartel 2004; Zhang and Wang 2015). Till date, about 40 different families of miRNAs have been shown to play a role in abiotic stress response among which many are associated with salt stress (Covarrubias and Reyes 2010; Sunkar 2010; Wang et al. 2013). *Arabidopsis* and rice have come up as a model system in recent times to study molecular biology of dicotyledonous and monocotyledonous plant systems, respectively. Numerous studies on these two plants have revealed the importance miRNAs in salt responses. Apart from these, the role of miRNA under salt stress has also been elucidated in several other crop plants like cotton, soybean, *Populus*, tobacco, *Medicago*, etc. About 217 miRNAs have been reported till date in different plant species which are involved in salinity stress. A detailed list of the salt-responsive miRNA and their target genes is given in Mittal et al. (2016). The unifying themes which emerge from the studies investigating the role of miRNA in response to salinity are summarized here. Firstly, it has been observed that miRNAs, grossly, target master switches of gene regulation such as transcription factors (e.g. MYB, NAC1, homeodomain-leucine zipper, etc.) or phytohormones (auxin, GA, ethylene and ABA signalling) which in turn regulate expression of several downstream genes in the expression cascade ultimately governing the plant development and physiology (Jones-Rhoades and Bartel 2004). Besides, some of these miRNAs regulate enzymes such NADP-dependent malic enzyme, cytochrome oxidase, laccase, etc. which are of broad spectrum and are involved not only in salt stress but also in several other abiotic and even in biotic stresses (Yan et al. 2005). Hence, most of the miRNAs are not specific to salt but are involved in multiple stresses; especially, several miRNA are commonly regulated in salt and drought stress (Kong et al. 2010; Xie et al. 2014). Secondly, it has been found that the stress-responsive miRNAs are more or less conserved in plant kingdom. For example, miR393 was found to be upregulated in rice, cotton and *Arabidopsis* under salt stress (Sunkar and Zhu 2004) and subsequently regulates auxin signalling in those plants (Xia et al. 2012). Similarly, salt-induced upregulation of miR156 is observed in seven different species, viz. *Arabidopsis thaliana* (Liu et al. 2008), *Zea mays* (Ding et al. 2009), *Populus euphratica* (Qin et al. 2011), *Vigna unguiculata* (Paul et al. 2011), *Panicum virgatum* (Sun et al. 2012), *Populus trichocarpa* (Li et al. 2013) and *Gossypium raimondii* (Xie et al. 2014). Several other miRNAs like miR159, miR160, miR162, miR164, miR166, miR167, miR168, miR169, miR395, miR397, etc. are also differentially expressed in multiple species under salt stress (Mittal et al. 2016). Combining these two facts, i.e. the evolutionary conserved nature and the overlapping expression pattern of miRNA in different stresses, it is intimidating to speculate that the miRNA-mediated gene regulation is an ancient phenomenon (relics of RNA world hypothesis?) which has probably originated as early as the plant kingdom made their existence in the world. And this regulation mechanism is not stress specific in most of the cases; rather it has been placed on top of the specific stress regulation mechanisms in order to combine and coordinate plants' response under multiple stresses.

14.4.4 Important Genes and/or QTLs Associated with Salt Tolerance and Ion Homeostasis

Genetically, salinity tolerance is a complex quantitative trait (Foolad and Jones 1993) which makes it difficult for plant breeders to select for improved genotypes due to low expressivity, heritability and large effects of environment on the trait. Still, genetic resources are vital for any trait, and intraspecific selection has contributed to improved tolerance in rice (Akbar and Yabuno 1977) and barley (Epstein et al. 1980). Over the past decade, research efforts have focused on the mapping and identification of QTLs contributing to salt stress tolerance through marker-assisted selection (Singh et al. 2007; Haq et al. 2010; Table 14.4). For example, the *Saltol* QTL in rice was identified by employing a RIL population between the tolerant landrace Pokkali and the highly sensitive IR 29 by AFLP genotyping (Gregorio 1997). Further, it was shown that the *Saltol* QTL contributed to 43% of variation for seedling shoot Na^+/K^+ ratio (Bonilla et al. 2002). Lin et al. (2004) identified a total of 11 QTLs from an F_2 population including major QTLs for shoot K^+ concentration on chromosome 1 (*qSKC-1*) and shoot Na^+ concentration on chromosome 7 (*qSNC-7*) as derived from a cross between tolerant indica rice (Nona Bokra) and sensitive japonica (Koshihikari). These QTLs were found to influence the root and shoot Na^+ and K^+ accumulation as well as survival under salt stress. Subsequently, a single QTL, *qSKC1* or *OsHKT1.5* was fine mapped and successfully cloned (Ren et al.

Table 14.4 QTLs governing tolerance to salinity stress in plants

QTL	Crop	Cross	Population	References
Kna 1	Bread wheat	–	Disomics for 4D/4B in genetic background of *Triticum turgidum*	Dubcovsky et al. (1996)
Na^+, Na^+:$K1^+$, Na^+: $K2^+$	Rice	IR4630/IR15324	RIL	Koyama et al. (2001)
Saltol	Rice	IR 29/Pokkali	RIL	Bonilla et al. (2002) and Thomson et al. (2007)
qSNC-7, qSKC-1	Rice	Nona Bokra/ Koshihikari	F2:3, BC_2F_2	Lin et al. (2004) and Ren et al. (2005)
Nax1, Nax2	Durum wheat	*Triticum monococcum*/durum cultivar Marrocos	BC_5F_2	Byrt et al. (2007)
HvNax3	Barley	CPI-71284-48/ Barque	F_2 and F_3	Shavrukov et al. (2010)
HvNax4	Barley	Clipper/Sahara 3771	DH	Rivandi et al. (2011)
QSl. TxNn.2H	Barley	TX9425/Naso Nijo	F1-derived double haploid (DH) lines	Xu et al. (2012)

2005). A list of some of the identified QTLs governing salt stress tolerance in different crop species is provided in Table 14.4, and a list of some experimentally validated gene involved in salt-induced response across plant species is given in Table 14.5. In rice alone, about 70 QTLs for salt stress have been mapped (Hu et al. 2012); however, cloning of QTLs is still a rate-limiting step, mainly due to difficulties in fine mapping and defining precise QTL limits. Hence, there is a need to direct research efforts towards identification of genes governing tolerance to salt stress which in turn would aid in development of perfect gene-based markers and pyramiding of multiple QTLs in a single genetic background so as to provide tolerance under diverse stress environments.

14.5 Cellular Defence Network and Plant's Adaptive Strategy

14.5.1 Role of Reactive Oxygen Species (ROS) in Salinity Tolerance

Salt stress disrupts metabolic coordination between different biochemical pathways, leading to formation of high-energy electrons which, when donated to molecular oxygen, result in the formation of different reactive oxygen species (ROS) such as $^1O_2$, H_2O_2, $O_2^{\bullet-}$ and $HO^{\bullet}$. The plant organelles, chloroplast, mitochondria and peroxisomes, are the sites of production of ROS in plants; however, detailed

Table 14.5 Key gene/gene families involved in governing response to salt stress

Gene/gene family	Role under salinity	References
Sensor proteins		
Salt overly sensitive 3 (*SOS3*)	Premier cytosolic Ca^{2+} sensor and activator of SOS pathway	Ishitani et al. (2000) and Gong et al. (2005)
OSCA1	Plasma membrane-bound calcium channel and putative osmosensor which directs osmotic stress-induced Ca^{2+} uptake in the cell	Yan et al. (2015)
AHK1/ATHK1	Osmosensor and positive regulator of osmotic stress response	Urao et al. (1999) and Tran et al. (2007)
Kinases		
Salt overly sensitive 2 (*SOS2*)	Belongs to sucrose non-fermenting-related kinase (SnRK1) group of proteins. Key component connects ABA-induced and Ca^{2+}-induced cell signalling under salt stress	Halfter et al. (2000) and Coello et al. (2010)
Calcium-dependent protein kinases (*CDPK*)	Transduce Ca^{2+} gradient- induced signal through a series of protein phosphorylation	Schulz et al. (2013)
Mitogen-activated protein kinases (*MAPK*)	Transduce environmental stress signal by a series of phosphorylation events of mitogen protein which ultimately culminates in the activation of TFs	Teige et al. (2004)
Histidine kinase (*HK*)	It is a kinase as well as an osmosensor. It functions as the receptors of ethylene and cytokinin	Urao et al. (1999) and Tran et al. (2007)
Ion channels		
Salt overly sensitive 1 (*SOS1*)	Na^+/H^+ antiporter localized in plasma membrane which governs the efflux of Na+ from the cell through active transport	Qui et al. (2002) and Brini and Masmoudi (2012)
$Na^+(K^+)/H^+$ exchanger (*NHX*)	Antiportes which maintains pH gradient and sequester Na^+ in the vacuole through active transport	Bassil et al. (2011) and Reguera et al. (2014)
High-affinity potassium transporters-1 (*HKT1*)	Governs the entry of Na^+ from soil solution or xylem into the root cell under high salinity	Rubio et al. (1995) and Byrt et al. (2007)
Non-selective cation channels (*NSCC*)	Governs Na^+ entry into the root under high salinity	Brini and Masmoudi (2012)
Transcription factor		
WRKY	Play role in regulating ABA-dependent abiotic stress responses	Chen et al. (2012)
MYB/MYC	Key element of the ABA-dependent signal transduction pathway under abiotic stress response	Abe et al. (1997)
bZIP	Involved in ABA-dependent signalling in responses to drought and high salinity	Uno et al. (2000)

(continued)

Table 14.5 (continued)

Gene/gene family	Role under salinity	References
NAC	Play role in both in ABA-dependent and ABA-independent abiotic stress response pathways	Nakashima et al. (2012)
CBF/DREB	Mediates ABA-independent gene expression regulation under osmotic stress	Agarwal et al. (2006)

biochemical reactions leading to their production are beyond the scope of this chapter. Both ROS formation and associated injury during salt stress in plants have been previously reported (Gomez et al. 2004; Rubio et al. 2009; Chen et al. 2012). ROS-induced damage in plants depends on the nature and severity of stress, the duration of exposure and even environmental conditions. However, it is well known that while ROS accumulation causes intracellular damage to lipids, proteins and DNA (Bi et al. 2009), it also functions as a signalling molecule in plant-pathogen interaction and abiotic stresses (Mittler et al. 2004; Torres and Dangl 2005). The plasma membrane-located NADP oxidase (*NOX*) genes or the respiratory burst oxidases (*RBOH*) which catalyse the synthesis of the superoxide radical are important constituents of ROS-mediated signalling system (Desikan et al. 2001; Mittler et al. 2004; Torres and Dangl 2005). Ma et al. (2012) reported that double mutants *atrbohD1/F1* and *atrbohD2/F2* of *Arabidopsis* disrupted Na^+/K^+ homeostasis therefore showing increased sensitivity to NaCl treatments than wild-type or single null mutants. *AtrbohF*, apart from increasing ROS levels in response to increased soil salinity, also reduced Na^+ concentrations in xylem sap and prevented accumulation of excess Na^+ in shoot cells through transpiration (Jiang et al. 2012).

Reactive oxygen species (ROS) scavenging is also extremely important for salt tolerance. The main defence against ROS includes enzymes such as ascorbate peroxidase (APX), superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), polyphenol oxidase (PPO) and monodehydroascorbate reductase (MDAR) along with low-molecular weight antioxidants such as ascorbate, glutathione, glycine betaine, trehalose, alpha-tocopherol and proline (Foyer and Noctor 2005; Abogadallah 2010). Overexpression of a rice ascorbate peroxidase gene in alfalfa led to improved salt stress tolerance. In rice transgenic overexpressing pea DEAD-box helicase gene *PDH45* which also showed improved salt stress tolerance, it was found that the protein PDH45 physically interacts with Cu/Zn SOD, adenosine-5′-phosphosulphate-kinase, cysteine proteinase and eIF(4G) thus implicating the role of ROS-scavenging machinery in stress tolerance (Gill et al. 2013). Transgenic tobacco plants overexpressing cotton type 3 metallothionein gene *GhMT3a* also showed increased tolerance against different abiotic stresses including salinity stress (Xue et al. 2009). Improved ROS scavenging may also be attained by manipulation of certain master regulator genes. For instance, Schmidt et al. (2013) identified a rice transcription factor, salt-responsive ERF1 (SERF1), that showed increased expression upon salt and H_2O_2 treatment. SERF1 showed direct binding to promoters of genes like MAPK kinase kinase 6 (*MAP3K6*), *MAPK5*, dehydration-responsive element binding 2A (*DREB2A*) and zinc finger protein 179

(*ZFP179*) thus suggesting that it may be the master regulator of ROS-activated MAPK cascade during the initial phase of salt stress making way for downstream gene expression changes resulting in salt stress tolerance.

14.5.2 Osmolytes or Compatible Solute-Mediated Adaptation to Salt Stress

Since osmotic imbalance is one of the most prominent effects of salt stress, adaptation to this stress, to a great extent, depends on the ability to mediate quick osmotic adjustment by accumulation of organic osmolytes like proline, mannitol, fructans, trehalose, glycine betaine, ononitol, etc. In fact, due to the importance of osmotic adjustment in salinity stress adaptation and in many other abiotic stresses as well, it has been regarded as the central dogma of stress physiology (Hare et al. 1998). Not many direct evidences, however, confirm this hypothesis, and most of the evidences are largely correlative. Exposed to salt stress, plants start accumulating organic osmolytes, most of which belong to the class of polyhydroxylic compounds (carbohydrates and sugar alcohols) and zwitterionic alkylamines (amino acids and quaternary amines), as an adaptive response. Unlike ROS, which can be potentially damaging to the cell itself, these organic osmolytes are non-toxic in nature and hence are also termed as ‘compatible solutes’. Cumulatively, these compatible solutes decrease the water potential of cell making them osmotically more competent for water uptake. Several reviews are available which discuss about osmolyte accumulation in plant (Bohnert and Jensen 1996; Serrano et al. 1998; Chakraborty et al. 2012b). Given their immense importance, osmolytes have emerged as tempting candidates to engineer stress resistance in crop plants. Several efforts have been made to develop transgenic plants containing osmolyte-synthesizing genes with an ultimate aim to engineer salt and/or drought stress tolerance. Few of such efforts have been successful (Hayashi et al. 1997), while many of them did not (Smart and Flores 1997). Even where some success has been achieved, the improvement was marginal. The limited success of the osmolyte-overexpressing transgenics is not a reason to dismiss their potential in engineering stress adaptation; rather it indicates the fact that the relative proportion of different osmolytes and the spatiotemporal expression of osmolyte-synthesizing genes are more important as compared to the absolute amount (Hare et al. 1998). Untimely, out of place and/or excessive expression of a particular osmolyte can be associated with yield penalty because of metabolite diversion from primary metabolism (which favours growth and yield) to secondary metabolism (which favours defence). Hence, it is imperative that future research needs to focus more on pathway engineering and devising controlled gene regulation machineries to achieve success in this area.

14.6 Possible Management Options for Alleviation of Salinity Stress

Apart from our traditional effort to breed salt-tolerant crop varieties, sometimes improved crop management practices also play important role in counteracting ill effect of salt stress. Hence, we should consider different external management approaches, viz. maintenance of K^+ homeostasis and the use of phytohormones for the growing plants in saline environment.

14.6.1 Exogenous Application of Potassium (K^+)

Around the world, researchers have attempted to alleviate the salinity stress applying potassium by and large. However, the mode of application varied over the experiments, either by soil or foliar application, while varying doses of sole potassium or in combination with some soil amendments (like FYM) or with external phytohormones. But some of the results obtained during the course of study are indeed exciting and hence addressing to solve the salt stress in crop plants by suitable crop management.

Salt stress is often noticed by the skewed K^+/Na^+ ratio in actively growing plant tissues along with stunted growth and metabolic activity of plant tissues (Shabala and Cuin 2008; Degl'Innocenti et al. 2009). Excess build-up of tissue Na^+ along with reduced uptake and tissue retention of K^+ in plant parts has been conspicuous under saline environment (Munns et al. 2002). Several basic physiological processes in plants, like stomatal closure, destruction of chlorophyll pigment system, etc., have been observed to be hampered under salinity (Gama et al. 2009; Parida et al. 2004). The role of K^+ is established in regulation of stomatal movement of plant tissue; thus, better maintenance of water storage and cell turgidity can be assured under osmotic stress (Marschner 2012).

Both soil and foliar application of K^+ supplemented the growth, yield and fruit quality of tolerant and sensitive cultivars of tomato grown under salinity. It ensured the role of external K^+ application apart from genetic tolerance ability to manage the stress (Amjad et al. 2014). Basal application of potassium improved the overall performance of contrasting peanut varieties at defined salinity levels, while TG 37A, the susceptible one, responded better over GG 2, the tolerant one (Chakraborty et al. 2016c). Similarly, Arshadullah et al. (2014) conducted a hydroponic study on sunflower crop and confirmed that 2% K^+ foliar application (as K_2SO_4 solution) revived the tissue K^+ concentration after imposition of salt stress, thus resulting in more biomass production.

In other study, Khan et al. (2016) reported that K^+ application along with FYM and other nutrients (N, P, Zn) enhanced the growth, yield and fibre quality of cotton plants by reducing the Na^+ uptake and Na^+/K^+ ratio under the salinity. While in most of the cases potassium sources have been restricted to KCl (muriate of potash) or

K_2SO_4 (potassium sulphate) salts, a recent study tested the K_2SO_4 nanoparticles on growth and physiological responses of forage crop, alfalfa (*Medicago sativa* L.), under salt stress, and subsequently better performance of nano-fertilizer was revealed by lower electrolyte leakage, higher proline and relative water content, along with higher antioxidant enzyme activities (superoxide dismutase and catalase), and other growth and yield parameters (El-Sharkawy et al. 2017).

14.6.2 Use of Phytohormones

Phytohormones, synonymously used as plant growth regulators, refer to the compounds originated from plant biosynthetic processes that can act either locally (at the site of their synthesis) or transported to some other sites within the plant in order to promote growth and development responses both under normal and adverse/stressful environment (Peleg and Blumwald 2011). A large array of phytohormones like abscisic acid (ABA), gibberellins (GA), ethylene, auxins (IAA), cytokinin (CKs), and brassinosteroids (BRs), has established their role in abiotic stress management (reviewed in Fahad et al. 2015). Moreover, salinity tolerance mechanism via proline biosynthesis as influenced by regulatory role of phytohormones under salinity stress has also been highlighted (reviewed in Iqbal et al. 2014). Kanmani et al. (2017) conducted a pot experiment with contrasting rice varieties (Pokkali and CO51) treated with foliar application of four different plant growth regulators for mitigating the stress. The response of brassinolide (1.0 ppm) was found interesting for photosynthetic rate and chlorophyll fluorescence, and gibberellic acid (50 ppm) increased the chlorophyll content, while enhanced transpiration rate was observed at kinetin application (20 ppm). In other instances, pretreatment with phytohormones (NAA and BAP) in pineapple (cv. MD Gold) minimized the salt stress effects suffered by the plant by maintaining optimum biomass, increasing tissue K^+ concentration, reducing the damage to cell membranes and increasing total soluble sugars (Melo et al. 2017).

14.7 Conclusion and Future Research Strategies

Salinity stress is second most important abiotic stress for cultivated crop plants. Salinity-affected area is gradually increasing under the scenario of global climate change. The importance of properly understanding and combating this threat to world agriculture is, therefore, more apprehended by the researchers. Soil salinity adversely affects plant growth and development accompanied by an increase in uptake of Na^+ and Cl^- ions and a decrease in uptake of K^+, Ca^{2+} and Mg^{2+} resulting in ionic imbalance, sodium ion injury and disturbed metabolic processes, changed concentration of biomolecules, photosynthetic activity and poor productivity. Other most detrimental effect faced by the plants is sudden outburst of reactive oxygen species produced due to salinity stress, which disrupts the cellular structure and damages subcellular organelles, leading to cell death. At molecular level, efficient operation of different signal proteins and various symporters and antiporters lying either in the plasma membrane or tonoplast plays important role in salinity tolerance. Activity of different Na^+/H^+ antiporters, viz. SOS1 and NHX1, depends upon the activation of other signal proteins like SOS2, SOS3 and other calcium-binding proteins.

The genotypes having superior antioxidant defence capacity in terms of either accumulation of antioxidants like ascorbic acid, glutathione, malondialdehyde, etc. or higher activity of the enzymes are more capable of withstanding salinity stress. Salinity stress causes osmotic and oxidative stress; hence, genetic modifications in these areas could yield beneficial result in bringing salinity tolerance in crop plants. Incorporation of genes facilitating biosynthesis of compatible solutes whose accumulation will help in osmotic adjustment in the plant cell and thereby maintaining better water balance inside the plant tissues when facing osmotic pressure from outside. Though there is ample opportunity for research in this area, it needs multidisciplinary approaches to address all the component of the problem of salinity.

Adaptation to salinity stress involves osmotic homeostasis, ionic homeostasis, ROS detoxification as well as tissue adaptation mechanisms. These adaptation strategies are governed by a network of several interacting pathways which are controlled by both genetic and epigenetic regulations. In this context, many cultivated accessions were identified with tolerance to salinity stress. QTLs for salt tolerance have been identified from those cultivated accessions. A few of these have been identified, mapped, cloned and introgressed into elite varieties using molecular breeding approaches. Satisfactory progress in transferring tolerance to high-yielding cultivars for better survivability is made. But yield penalty under salinity stress can’t be reduced significantly. In this context, some of the wild relatives with better tolerance are being utilized in breeding. The major setback faced by the breeders in this approach is that most of wild tolerant genotypes are often cross-incompatible with the cultivated species. There is a need to go for mining of the differentially expressed genes and subsequent transfer of those to cultivable species.

The search for novel salt-tolerant genes or protein is presently extended to some of the halophytic plants such as mangroves which can thrive well under extremely saline environment. The successful transfer of the important genes imparting tolerance to soil salinity from mangrove gene pool to some of important crop plants is being attempted. Besides this, mining of the genes is also possible from a wide range of microbial gene pool as well as from *Archaea*. Apart from the commonly known pathways that impart tolerance to eukaryotes including higher plants, there may be some other mechanisms operating in these organisms which help them to survive in the extreme environment of sea or saline hot spring. During the past few decades, ‘omics’ approaches have opened possibilities of understanding interaction dynamics between genes, proteins, metabolites and small RNA in salinity stress tolerance both under acute and chronic salinity stress. Recent advent of ‘phenomics’ or large-scale phenotyping is expected to further facilitate efficient identification of promising germplasms for enhancing salt stress tolerance. But the progress made so far is still at the infant stage, and mechanisms of salinity tolerance at the morphological, physiological and molecular level are not very well deciphered in all the crops. It is understood that salinity tolerance like other complex abiotic stress tolerance is controlled by many environmentally responsive genes. Many of them are affected by the occasional post-transcriptional modifications due to extreme climatic fluctuation. Under global climate change, 'envirotyping' is emerging as a new concept which will predict multiple genes more precisely along with genotyping and phenotyping and haplotypes interacting with environments across developmental stages. This will help in understanding and genetic manipulation for achieving better salinity tolerance. Besides the potential crosstalk of salinity stress regulatory circuit with other pathways governing the overall physiology of the plants is still mostly under cover. Hence, in-depth studies by means of real-time and cutting-edge technologies at cellular and at the whole-plant level is essentially required in the days to come to have a complete understanding for developing salt-tolerant and environment-resilient varieties in the future.

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Chapter 15

Role of Micronutrients in Salt Stress Tolerance to Plants

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Abstract Salt stress is an important abiotic stress factor which decreases the crop yield and quality. About 23% of cultivated lands are saline all over the world. The direct effects of salt stress on plants are reduced photosynthesis, respiration, and nutrient assimilation as well as hormonal imbalance. Indirect adverse effect of salinity is oxidative stress, which is enhanced by the generation of reactive oxygen species (ROS) in stressed plants. The ROS production subsequently causes damage to macromolecules such as lipids, proteins, and nucleic acids and thus disturbs membrane permeability. Salt stress conditions adversely affected essential nutrient availability and consequently crop yield and quality. Nutritional disorders are very common under salinity due to non-availability of nutrients and their competitive uptake and transport in plants. Micronutrients can mediate adverse effects of salt stress. Micronutrients (Mn, Zn, Fe, B, Cu, Cl, Ni, Mo, etc.) play different roles in mediating salt stress due to their involvement in diverse mechanisms, i.e., reduced ion toxicity, maintenance of water balance, improved mineral uptake and assimilation, biosynthesis of compatible solutes plus phytohormones, modification of different gas exchange attributes, and decrease in oxidative stress plus modification of gene expressions.

Keywords Mediated salinity tolerance · Micronutrients · Mineral elements · Salt stress · Uptake and transportation

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15.1 Introduction

Plants face numerous abiotic stresses, which decrease their growth and yield. Among different abiotic stresses, salt stress severely reduced crop yield (Hasanuzzaman and Fujita 2011, 2012; Hasanuzzaman et al. 2012, 2013a, b, c, 2017a, b). In the world, about 23% of total cultivated land is salt affected and 37% is sodic. About 20 million hectares of land is salt affected, and no crop is cultivated on that land. In Asia and Africa, this problem is more severe due to the shortage of water (Francois and Maas 1999). In Pakistan, about 6 million hectares is salt-affected land (coastal and inland areas) with no cultivation (Anonymous 1999).

The crop yield and quality are severely hampered under salinity (Hasanuzzaman et al. 2013a, b). Salinity affected the nutrient dynamics in soil solution, which disturb the different nutrient uptake and assimilation. In plants, under salinity, micronutrient uptake and assimilation are highly variable (Grattan and Grieve 1992). In citrus under salt stress conditions, the decrement is observed in the uptake and assimilation of different micronutrients. The growth and yield of citrus plants decrease due to reduction in net assimilation rate and photosynthesis (Romheld and Marschner 1986).

Different researchers studied the concentration of micronutrients, their uptake, and assimilation as affected by salinity, which ultimately hindered growth and yield of plants (Bañuls et al. 1990; El-Fouly et al. 2010). Among different methods to increase the salt tolerance in plants, foliar spray of micronutrients mediates the salt stress by easing Na^+ plus Cl^- injury to plants (El-Fouly et al. 2010). Under high salinity, nutrient uptake is limited in root medium. Generally, the uptake and assimilation of nitrogen (N), phosphorus (P), potassium (K), magnesium (Mg), and calcium (Ca) tend to decrease with increase in salinity levels.

15.2 Effect of Salinity on Uptake of Micronutrients

Salinity adversely affect crop performance by altering nutritional disorders like availability of micronutrients, competition in their uptake, assimilation, and movement in plants (Table 15.1). Salinity increases level of sodium (Na) and chloride (Cl) ions in plant which have direct impact on concentration of other micronutrients. Uptake and movement of Ca in plant are decreased by increase in the concentration of Na, which affects yield and quality (Grattan and Grieve 1999). Under salinity, micronutrient concentration varies in different plant species. Mn and Zn concentration is increased in barley, tomato, and rice under salinity whereas decreased in corn shoot (Hassan et al. 1970; Mass et al. 1972). In shoots of pea, tomato, and rice, Fe concentration is increased (Dahiya and Singh 1976; Mass et al.

Table 15.1 Micronutrient level as affected by salinity in different plant parts

Micronutrients	Plant part	Level	Crop	References
Manganese (Mn) and zinc (Zn)	Shoots	Increased	Barley	Hassan et al. (1970)
			Tomato	Mass et al. (1972)
			Rice	Verma and Neue (1984)
		Decreased	Corn	Hassan et al. (1970)
Zinc (Zn)	Roots	Increased	Tomato	El-Fouly et al. (2002)
Manganese (Mn)	Leaves	Decreased	Tomato	El-Fouly et al. (2002)
	Roots	Decreased	Tomato	El-Fouly et al. (2002)
Iron (Fe)	Shoots	Increased	Pea	Dahiya and Singh (1976)
			Tomato	Mass et al. (1972)
			Rice	Verma and Neue (1984)
		Decreased	Barley	Hassan et al. (1970)
			Corn	Hassan et al. (1970)
	Leaves	Decreased	Tomato	El-Fouly et al. (2002)
	Roots	Decreased	Tomato	El-Fouly et al. (2002)
Boron (B)	Shoots	Decreased	Wheat	Holloway and Alston (1992)
Copper (Cu)	Leaves	Decreased	Tomato	El-Fouly et al. (2002)
	Roots	Decreased	Tomato	El-Fouly et al. (2002)

1972) while decreased in corn and barley (Hassan et al. 1970) under salinity. El-Fouly et al. (2002) observed the increment of Zn concentration in the roots of tomato under salinity. He also reported that tomato grown under salinity showed decrement in Mn, Fe, and copper (Cu) contents in leaves and roots.

The leaves of two mango rootstocks (Gomera-1 and Gomera-2) under salt stress showed increment in Mn, Fe, Ca, Zn, P, K, and Cu while decrement in Mg concentration. Similarly, Ca, Mg, N, and Cu contents are increased in stem, but Zn contents decrease in stem. Roots of these rootstocks showed increase in N, Fe, Cu, and Mn contents, while, P, K, and Mg were decreased. The concentration of micronutrients is more in fibrous roots as compared to main roots (Zuazo et al. 2004). The micronutrient uptake was different in plant organs when grown under saline environment. Furthermore, in soybean, the concentration of Fe, Mn, Cu, and Zn was more in roots as compared to leaves plus shoots (Tuncturk et al. 2008).

Salt stress also imposes drought which can also affect nutrient uptake and assimilation. Under severe salinity, the plant growth and yield are not increased by increasing nutrient concentration in soils, because under salt and drought conditions nutrient uptake is low. Hence, understanding the role of micronutrients in plant resistance to salinity will help to improve the fertilizer management in arid plus semiarid areas (Hu and Schmidhalter 2005).

15.3 Mechanisms of Micronutrient-Mediated Salinity Tolerance

15.3.1 Reduction of Ion Toxicity and Maintenance of Water Balance

Growth and development of the plants are associated with the physiological responses that are associated with ion accumulation. Macro- and micronutrients essential to plants compete in their uptake and metabolism under salinity (Wang et al. 2003). Increase in specific ion accumulation like sulfate (SO_4^{2-}), chlorine (Cl^-), and sodium (Na^+) caused toxicity, which ultimately decreased the uptake of different nutrients like potassium (K^+), calcium (Ca^{2+}), P, and N. Plants are sensitive to high Na^+ plus Cl^- contents in soil, which ultimately decrease growth and yield. Tavakkoli et al. (2011) studied the toxicity effect of Na^+ plus Cl^- in four barley cultivars and observed a decrease in growth plus yield. High contents of Na^+ plus Cl^- in soil decreases the uptake and assimilation of K^+ plus Ca^{2+} which results in reduction of photosynthesis, stomatal conductance, and chlorophyll (Tavakkoli et al. 2011; Fig. 15.1).

In *Atriplex griffithii* high Na^+ and Cl^- concentration was observed in leaves and then shoots and roots under salinity. This increment in Na^+ plus Cl^- decreases Ca^{2+},

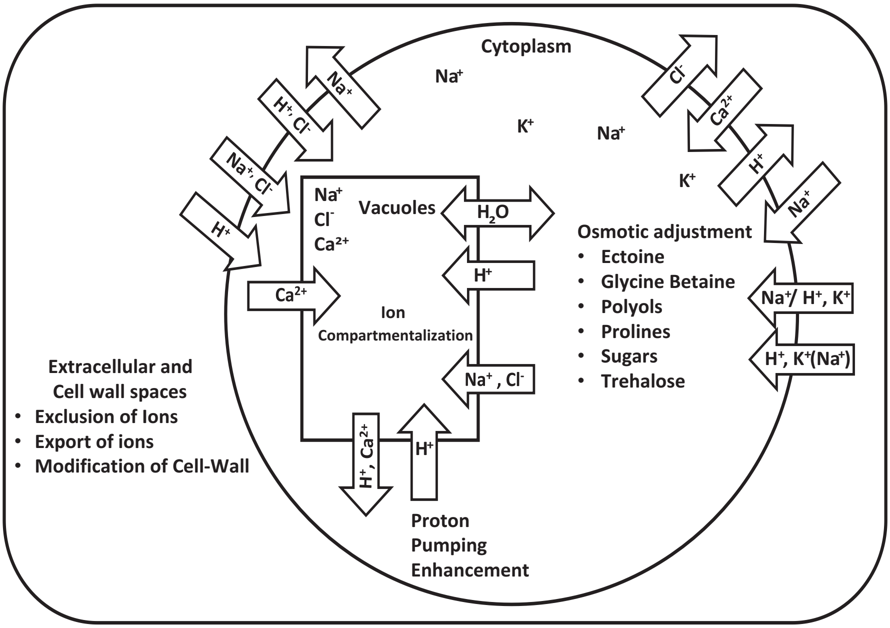

Fig. 15.1 Three sections of plant cell. (i) Extracellular and cell wall spaces, (ii) cytoplasm, and (iii) vacuoles. Na^+ and Cl^- movements across membranes and ion compartmentalization in vacuoles

K^+, and Mg^{2+} contents which shows the negative relation of these ions under salt stress and leads toward decrease of chlorophyll contents (Khan et al. 2000). During the initial stage (seedling and primary vegetative stage), plant is particularly more sensitive to salt stress. Hasanuzzaman et al. (2009) observed that plant height, leaf area, and tiller number significantly decrease in the rice under salinity. Similarly, Guan et al. (2011) observed that plant height, length and number of branches, and shoot diameter decreased by more accumulation of Na^+ and Cl^- contents in *Suaeda salsa*. Dolatabadian et al. (2011) and Semiz et al. (2012) also observed substantial decrement of plant weight (root and shoot), number of leaves, plant biomass, and yield.

However, many different mechanisms like restrictions in uptake and movement of salts in plants, maintenance of essential element ratio during salinity, and extrusion of salt from plants are involved for tolerance in salt stress to overcome toxicity of ions and withstand homeostasis (Parida et al. 2004). Micronutrient foliar application enhanced the root growth and decreased the nutritional disorder symptoms (El-Fouly et al. 2010). It increases the uptake of micronutrients in roots and decreases the effect of salt.

Fe is an important micronutrient essential for chlorophyll synthesis. Furthermore, Fe is an important part of the plant enzymes that play an important role in photosynthesis plus respiration (Curie and Briat 2003). Similarly, Mn also plays an important role as an activator of various enzymes and takes part in photosynthesis and also a constituent of photosystem II protein and activates decarboxylase, dehydrogenase, superoxidase, and phosphatase. Mn deficiency inhibits growth and induces chlorosis, necrosis, and leaf fall (Sajedi et al. 2009).

15.3.2 Improved Mineral Uptake and Assimilation

In plants, relation between uptakes of mineral nutrients under salt stress is multifarious. Salinity affects the availability of nutrients, their uptake, and transport within plant. Salt stress decreases uptake of mineral nutrients, which strictly affects crop productivity (Rogers et al. 2003; Hu and Schmidhalter 2005; Table 15.2). The uptake and assimilation of micronutrients under salt stress depend upon genotype and salinity level (Oertli 1991). There are many factors affecting the availability of micronutrients under salt stress. Under salt stress conditions, micronutrient availability depends upon micronutrient solubility, soil solution pH, redox potential, and nature of binding sites. In saline soils, micronutrient solubility is predominantly low, and plants frequently experience deficiencies, however not in all cases (Page et al. 1990).

Salinity severely affects the uptake and assimilation of Cu. In leaves and stem of salt-stressed maize, the concentration of Cu is decreased. In contrast, the Cu concentration in leaves of tomato grown hydroponically increased under salinity (Izzo et al. 1991). Similarly, the Mn showed decrement in the shoot of maize and tomato (Izzo et al. 1991; Rahman et al. 1993). On the other hand, in leaf and shoot of tomato plant, increase in Mn concentration is observed under salt stress (Niazi and Ahmad 1984).

Table 15.2 Effect of micronutrient spraying on micronutrient uptake (Fe, Mn, Zn, and Cu) μg/pot of tomato plants under different levels of NaCl salinity (El-Fouly et al. 2002)

Treatment	Micronutrient uptake (μg/pot)			
	Fe	Mn	Zn	Cu
Leaves				
Control	939	846	161	26
3000 ppm NaCl	703	118	142	13
Control + Mn	1310	1035	247	33
3000 ppm NaCl + MN	773	590	178	25
Stems				
Control	431	189	156	9
3000 ppm NaCl	393	87	113	6
Control + Mn	348	254	192	11
3000 ppm NaCl + MN	420	131	139	7
Roots				
Control	565	258	161	90
3000 ppm NaCl	441	217	193	35
Control + Mn	1209	384	299	58
3000 ppm NaCl + MN	803	254	239	130

MN = Micronutrient (Fe2.8%, Mn 2.8%, and Zn 2.8%)

High pH is the major factor, which causes deficiency on micronutrient. The micronutrients are most available under the soils having less pH. In high-pH soils, there is less availability of ions like Fe, Mg, Zn, and Cu. Under salt stress, pH of soil is elevated, and availability of micronutrients becomes less because the ionic form of micronutrients is transformed to the oxides or hydroxides. Under salinity by maintaining soil pH, we will enhance the uptake and assimilation of micronutrients to plants. The uptake and assimilation of P also decreased with increasing salt stress. Under salt stress conditions, phosphorous availability is low due to reduction in PO_4^{3-} activity, less solubility of Ca-P, and absorption process (Qadir and Schubert 2002). The growth and yield of the crop are damaged by decrease in N uptake which is mainly affected under salinity by the interaction of Cl^- and NO_3^- or Na^+ and NH_4^+ (Rozeff 1995). Hussin et al. (2013) reported that, by increasing salinity, calcium and magnesium ion concentration is decreased. As increasing concentration of salts in soil, the sodium level is elevated, which ultimately reduced the assimilation of potassium and calcium by which the imbalance of K, Ca, and Mg ions occurs (Keutgen and Pawelzik 2009). Calcium, nitrogen, and potassium ion concentration is decreased by increasing the level of sodium in saline soils (Tuna et al. 2007).

Salinity increases the concentration of Zn in citrus (Ruiz et al. 1997), maize (Rahman et al. 1993), and tomato (Knight et al. 1992), while decreases Zn in cucumber leaves (Al-Harbi 1995). Iron concentration in plants under salinity is as inconsistent as Zn and Mn. It has been reported that under salinity, Fe, Mn, Cu, and Zn were higher in roots than leaves and stem in soybean (Tunçturk et al. 2008). The nutrient uptake in various organs of faba bean was decreased by increasing salinity.

El-Arquan et al. (2002) found that N, P, and K uptake were decreased under salt stress. Thus, excessive Na^+ plus Cl^- in soil solution reduce the uptake and translocation of nutrients (Thalooth et al. 2006). El-Fouly et al. (2002) described foliar application of micronutrients increased the nutrient uptake under salinity.

Micronutrient foliar sprays showed positive effects with different degrees on micronutrient uptake when sprayed either before or after the salinization treatments. Exogenous application of micronutrients can mediate adverse effects of salinity by improving root growth, preventing nutritional disorders, and therefore increasing uptake of nutrients (El-Fouly et al. 2002).

Sodium concentration of different plant organs of faba bean seedlings was increased in the presence of NaCl in growth medium (El-Fouly et al. 2010). Spraying plants with a micronutrient compound after salinity treatment leads to a reduction of Na concentration on roots and leaves, while it was increased and accumulated in the stem. Micronutrient foliar applications lead to the decrease of Na^+ ion concentrations. This may contribute to the reason that micronutrients have a regulatory mechanism and/or a control function on Na uptake and translocation rate. Micronutrients may be involved in integrity plus function of biomembrane in plants (Thalooth et al. 2006).

Increasing NaCl concentration leads to the decrease of K/Na and Mg/Na ratios. The decrease may be attributed to increase of Na^+, which diminished concentration of K^+ plus Mg^{2+} due to antagonistic interaction. Spraying plants with a micronutrient compound after salinity treatment leads to the reduction of Na concentration in roots and leaves, while it was increased and accumulated in the stems (El-Fouly et al. 2010). Consequently, K^+/Na^+ plus Mg^{2+}/Na^+ ratios in the roots and leaves showed high values and were reduced in the stem. Foliar sprays of micronutrients under salinity increase the ability of roots for selectivity of potassium plus magnesium ions, which allows transportation maintenance of both ions and limitation of sodium ion uptake in the shoots (Tattini et al. 1993; Carvajal et al. 1999). In this respect, K/Na ratio might be considered as a tool of plant tolerance to salt stress.

15.3.3 Biosynthesis of Compatible Solutes and Phytohormones

During salt stress conditions, plant absorb more salts which decrease its osmotic potential. To cope with this problem, plants absorb inorganic salts like osmolytes and hydrophilic proteins that maintain osmotic relation. When plants are exposed to salinity, different osmolytes increased like proline and glycine betaine. To overcome these osmolytes, there is need of some enzymes, and under salinity, concentration of these enzymes also decreased (Pang et al. 2010). Askari et al. (2006) found that these enzymes are involved in glycine betaine synthesis under salt stress: Sadenosylmethionine synthetase (SAMS) and betaine aldehyde dehydrogenase (BAD). Hydrophilic proteins including dehydrins have been observed to be elevated under salt stress (Kosová et al. 2010). Salt-inducible LEA proteins, dehydrin*TAS14*, was observed by different scientists in tolerant genotypes of rice and tomato (Godoy et al. 1994). Wu et al. (2013) also found that under salt stress, different compatible solute concentrations are increased like proline, glycine betaine, sugars, etc.

Under salt stress conditions, plants also increased the production of several enzymes which are involved in phytohormone metabolism like jasmonic acid (JA) biosynthesis (allene oxide cyclase, AOC; lipoxygenase, LOX), gibberellin (GA) biosynthesis (*DWARF3*), ethylene biosynthesis (*SAMS*), and ABA biosynthesis (9cisepoxycarotenoid dioxygenase, NCED). Activation of JA (increase in AOC and LOX levels) in salt-treated *A. thaliana* that indicates a better relative abundance of JAinduced signaling under salinity has also been reported (Pang et al. 2010). Increased abundance of abscisic acid (ABA) biosynthesis found in *T. salsuginea* (Taji et al. 2004) relates with enhanced ABA levels observed in salt-affected plants and with an increased expression of numerous ABAdependent transcription factors and ABAresponsive genes. An improved induction of ethylene receptor *ETR1* was found in wheat under salinity (Peng et al. 2009).

Micronutrients improve plant tolerance against salt stress through activating some osmoprotectants. Iron, zinc, and manganese increase the proline concentration which can tolerate the effect of salts (Babaeian et al. 2011). Iron also increases production of proteins under salinity (Jalilvand et al. 2014).

15.3.4 Modification of Gas Exchange Attributes

Salinity decreased the photosynthetic process and other gas exchange attributes which ultimately decrease yield and lead to death of plant. Decreased photosynthesis performance of salt-stressed seedlings possibly offered an explanation that diminished exploits of energy toward sustaining photochemical reactions (Wang et al. 2014).

Plants have different pathways (photosynthesis) which help them to grow. In photosynthesis, conversion of solar energy to chemical energy is done. Under salinity, plant losses its water potential, which ultimately gives a negative impact on photosynthetic process. As discussed earlier, by increasing the salinity, elevation in Na^+ and Cl^- ions occurs by which plant decreases its chlorophyll contents which is the main indication of plant at cellular level under stress (Chutipaijit et al. 2011). The decrement in chlorophyll contents is directly associated with the photosynthesis (Zhang et al. 2005). Amirjani (2011) and Chutipaijit et al. (2011) in rice observed the decrease in chlorophyll contents under salinity. They also reported that by increasing salt stress, the chlorophyll “a” and “b” contents decrease. The decreases in chlorophyll pigment ultimately decrease the net photosynthetic rate, transpiration, and stomatal conductance.

Many reasons are involved in degradation of chlorophyll among which deterioration of membrane is one of them (Mane et al. 2010), by which the photosynthesis, transpiration, and stomatal conductance are decreased. A key role is played by Fe in chlorophyll synthesis. Iron enters in numerous plant enzymes, which play leading roles in oxido-redox reactions of respiration and photosynthesis (Curie and Briat 2003).

Under saline conditions, photosystem II (PS II) is comparatively more sensitive (Allakhverdiev et al. 2000). Piotr and Grazyna (2005) noticed that efficiency of electron transport chain (ETC), PS II, and CO_2 assimilation is decreased under salinity. Declined biomass is also observed by Demetriou et al. (2007). He reported that under salt stress, alteration in photosystem decreases the plant biomass. Kalaji et al. (2011) in barley, Mittal et al. (2012) in brassica, and LòpezCliment et al. (2008) in citrus observed that under salt stress condition photosynthesis, function of oxygen-evolving complex, stomatal conductance, efficiency of photosystem, and chlorophyll florescence are decreased which ultimately decreases the growth and yield of the crop.

Decline in photosynthetic rate is mainly done by salt toxicity; changes in cytoplasmic structure, decrease in source sink relation, and loss of turgor in cell membrane which ultimately decrease the permeability to CO_2 in cell are the factors which damaged the photosystem of plant under salinity (Iyengar and Reddy 1996).

Micronutrients ultimately decreased the effect of salinity (El-Fouly et al. 2002). Foliar application of micronutrients mediates metabolic disorders like low photosynthetic rate associated with high respiration which have a high impact on yield (Porath and Poljakoff-Maybee 1968). Iron and Mn play very important role in the activation of different enzymes that take part in photosynthesis plus respiration (Curie and Briat 2003). Iron is present in redox center of proteins that is essential for photosynthesis plus cellular respiration (Gross et al. 2003).

15.3.5 Reduction in Oxidative Stress

The plants under salinity face numerous problems, and accumulation of reactive oxygen species (ROS) is one of them. ROS mainly damage the DNA and other vital organs of plants. By accumulation of ROS, lipid peroxidation, accumulation of hydrogen peroxide, inactivation of enzymes, and denaturing of proteins are done in plant cells (Hasanuzzaman et al. 2012). ROS are mainly produced by less availability of CO_2 in plant cell. Under salinity the stomata are closed that decrease the level of CO_2 which leads toward the less carbon fixation and production of ROS like superoxide ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), hydroxyl radical ($OH^{\bullet}$), and singlet oxygen (Ahmad et al. 2011). ROS production in salt stress conditions is one of main factors which decrease the growth and yield of the crop (Asada 1994). Consequently, ROS regulation is a critical procedure to avoid cellular toxicity plus oxidative damage (Halliwell and Gutteridge 1989).

Salinity also imposes the drought effect to plant which is also a major factor of ROS production and metabolic activities (Cheeseman 1988). In many plant species under salt stress conditions, the ROS productions are observed which act as a mediator in membrane damage and cellular toxicity. When wheat plant is exposed to salt stress conditions, the MDA and H_2O_2 contents are significantly increased which damage the membrane of cell (Sairam et al. 2002). Hasanuzzaman et al. (2011) also observed the increment of lipid peroxidation (MDA) and hydrogen peroxide (H_2O_2)

under salinity stress in *Brassica*. Application of Se can decrease the production of ROS by activating the antioxidant defense mechanism under salt stress. Superoxidase dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate (APx), and glutathione (GPx) are the enzymes that activate and decrease the production of ROS (Hasanuzzaman et al. 2011).

15.3.6 Modification of Gene Expressions

Tolerant plants have stress-responsive genes which express under different stress conditions and these genes are absent in sensitive plants. So there is clear difference at genomic level. To reveal the signaling networks that control stress tolerance at genome level must be done by profiling or systematic genetic analysis. Salt-tolerant genes have different mechanisms or process. Some genes control uptake and accumulation of salts, some genes activate and make a plant grow under salt stress conditions, and some genes have protective and osmotic function (Munns 2005). Different micronutrient uptake takes place by different genes as Fe uptake from soil to root takes place by *IRT1* gene (Eide et al. 1996). The other gene *IRT2* is responsible for root iron transport (Vert et al. 2002). Under salt stress, these genes can tolerate salinity by uptake of iron.

15.4 Conclusions and Future Prospects

Salt stress conditions strictly affect the crop growth and its productivity. Salt stress directly influences on assimilation of nutrients, hormonal imbalance, stomatal conductance, photosynthetic rate, respiration, etc. Reactive oxygen species (ROS) are also generating under salt stress conditions which ultimately damage the plant cell and especially lipids, proteins, and DNA. Salinity also causes nutrient imbalance which can alter plant growth. Micronutrients play an important role in tolerance of plant against salinity. Different micronutrients play different roles in activation of enzymes which take part in different metabolic processes. Further studies are required to explore the more specific role of micronutrients, their mechanism, and pathways as well as their uptake under abiotic stresses especially under salinity.

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Chapter 16
Role of Beneficial Trace Elements in Salt Stress Tolerance of Plants

Aditya Banerjee and Aryadeep Roychoudhury

Abstract A large proportion of the global cultivable land is inflicted with salt stress. Plants, especially crop species, are usually sensitive to high saline conditions. As a result, crops grown in saline areas succumb to premature wilting, leading to large-scale yield losses. Hence, there is an urgent requirement of an economic and easy technology to sustain crop development even in suboptimal conditions. Trace elements are micronutrients which are beneficial for plant growth and physiology at very low concentrations. Existing reports suggest that exogenous application of some of these trace elements ameliorates salt sensitivity in a species- and cultivar-dependent manner. Optimum concentrations of such micronutrients act as supplements for the system. Trace elements promote plant growth, photosynthetic efficiency, and water usage during salinity. The accumulation of the compatible solutes and the nonenzymatic components of the antioxidant machinery are triggered. The activities of the enzymes belonging to the antioxidant system are also enhanced in the presence of exogenous trace elements. Increased accumulation of toxic reactive oxygen species (ROS) is counteracted through their effective scavenging by means of several antioxidants. Some trace elements also stabilize the cell wall and promote systemic integrity under salt stress. This chapter exclusively discusses the beneficial effects of essential and quasi-essential trace elements like magnesium, zinc, iron, selenium, silicon, boron, and iodine in conferring plant tolerance against salt stress.

Keywords Trace elements · Micronutrient · Salt stress · Exogenous application · Physiology · Antioxidants · Tolerance

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16.1 Introduction

Essential elements are extremely important for sustaining the proper development of an organism throughout its life cycle. Almost 17 essential elements are known to support the normal physiology of a plant, and these have been subsequently divided into macro- and micronutrients (trace elements) depending on their abundance in the system. Elements like C, H, O, Ca, K, Mg, N, S, and P present at >1000 mg kg^{-1} of dry weight and constituting >95% of dry matter are referred to as the macronutrients (Watanabe et al. 2007). On the contrary, the trace elements like Cl, B, Cu, Fe, Mn, Mo, Ni, Zn, Si, Se, etc. are typically detected at <100 mg kg^{-1} of dry weight. These micronutrients are required at extremely low levels for plant survival (Watanabe et al. 2007). The trace elements which act as growth promoters under variable abiotic stress conditions like salt stress are immensely beneficial for the plants.

Sessile organisms like plants remain affixed to a substratum and are exposed to high salt toxicity in the soil. It is a major edaphic adversity prevalent in specific parts of the globe. The UNESCO Water Portal (2007) has estimated that >6% of the total land and 30% of the irrigated land areas have salt content unsuitable for agricultural pursuits. An increase in aridity in the Mediterranean region and the semiarid regions of the earth in the near future has been postulated by the Intergovernmental Panel on Climate Change (2007). These constraints limit the global agricultural expansion, leading to an overexploitation of natural resources to feed the ever-growing population (Banerjee and Roychoudhury 2017a).

The mechanisms that dictate the developmental effects of trace elements have been studied by observing the phenotypic differences between plants growing in the absence or presence of the micronutrient (Pilon-Smits et al. 2009). Trace elements which accumulate in leaves at high concentration under abiotic stresses confer osmotic protection and act as crucial cofactors for several enzymes. Exogenous treatment with the optimum concentration of the beneficial micronutrient in plants belonging to specific taxa might supplement a metabolic pathway and promote growth (Pilon-Smits et al. 2009). Studying these positive effects is important in the context of plant ecology, since beneficial trace elements aid the plants to tolerate suboptimal conditions like salinity. The present chapter deals with a concise discussion on the salinity-induced damages during plant development and their amelioration by beneficial micronutrients like selenium, silicon, zinc, manganese, iron, boron, and iodine.

16.2 The Salt-Induced Physiology in Plants

High salt concentration negatively regulates plant growth by causing imbalance in the osmotic equilibrium within the cells. In response to salt stress, the plants mediate osmotic adjustments via the reduction of cell division, expansion, and stomatal closure and by modulating physiological parameters like reducing leaf area to minimize transpiration. Overall photosynthetic efficiency also decreases as a result of which the growth rate declines (Banerjee and Roychoudhury 2017a). Limited photosynthetic area is unable to support the normal growth of the salt-inflicted plants, leading to premature senescence of adult leaves (Nahar et al. 2016). Prolonged exposure to salt leads to the accumulation of Na^+ and Cl^- at toxic levels, accompanied with uncontrolled efflux of K^+, which induces ionic stress (Rahman et al. 2016a). It has been observed that high Na^+/K^+ ratio is toxic for the cell as the Na^+ ions outcompete K^+ ions for binding sites of essential enzymes and the Na^+ ions cannot be a substitute for K^+ (Rahman et al. 2016b). The osmotic stress is triggered by uncontrolled accumulation of reactive oxygen species (ROS) like superoxide radicals, hydrogen peroxide (H_2O_2), hydroxyl radicals (OH^-), etc. which disrupt the membrane architecture and other essential physiological processes (Hasanuzzaman et al. 2013). Oxidative damages during salt stress can also be carried out by cytosolic compounds like methylglyoxal (MG) (Hasanuzzaman et al. 2014).

Plants have evolved strategies to counteract salt-induced damages. Production of compatible solutes like proline (Pro), polyamines (PAs), glycine betaine (GB), etc. regulates the osmotic homeostasis by chelating the ROS (Roychoudhury et al. 2015; Roychoudhury and Banerjee 2016). The compatible solutes maintain osmotic homeostasis by stabilizing the biomacromolecular protein complexes and the water relationship. Salt-tolerant plant varieties have active antioxidant machinery which efficiently scavenges the toxic ROS. Ascorbic acid (AsA), glutathione (GSH), phenolics, alkaloids, tocopherols, and free amino acids constitute the nonenzymatic fraction of this machinery (Roychoudhury and Banerjee 2015). The enzymatic participants are superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), guaiacol peroxidase (GuPX), and glutathione-S-transferase (GST) (Hasanuzzaman et al. 2012). Several osmotic responsive (*OR*) genes which encode products like late embryogenesis abundant (LEA) proteins, etc. are also upregulated during salinity stress (Banerjee and Roychoudhury 2016).

Salt stress induces epigenomic alterations at multiple loci like cell wall-related *ZmEXPB2* and *ZmXET1*; histone acetylases, *ZmHATB* and *ZmGCN5* in *Zea mays*; histone deacetylases, *HD2C*, *HDA6*, and *HDA19* in *Arabidopsis*; abscisic acid (ABA)-associated *ABA1*, *ABA3*, and *Response to ABA 18* (*RAB18*); and *pyrroline-5 carboxylate synthase* (Banerjee and Roychoudhury 2017b, c; Banerjee et al. 2017). Rice cultivars grown under saline conditions exhibit differentially methylated regions (DMRs) which in association with transposons can be closely related to the transcript abundance of protein-encoding genes (Garg et al. 2015).

16.3 Trace Elements in Mitigating Salt Stress

The role of micronutrients in alleviating salinity stress in plants is less investigated. Some available reports show that trace elements exhibit positive effects in counteracting salt stress. In this chapter, we have exhaustively discussed on the mechanism

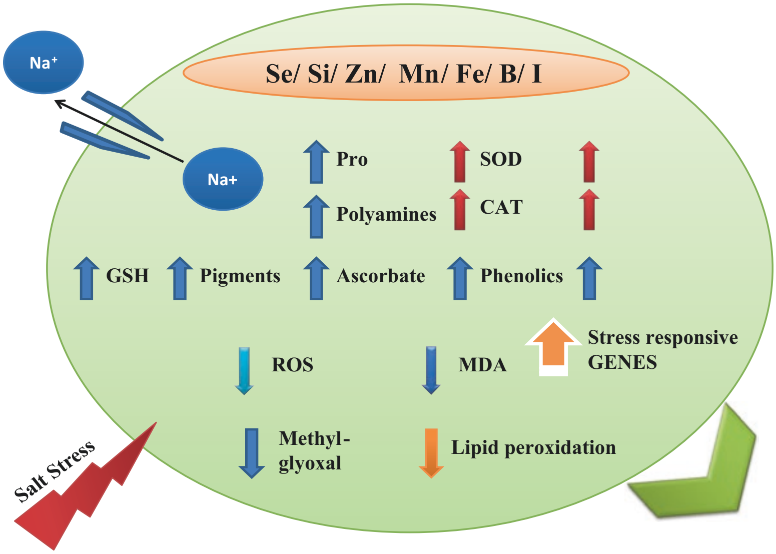

Fig. 16.1 The multiple cellular mechanisms by which trace elements mediate salt tolerance in plants. Se, Si, Zn, Mn, Fe, B, and I are reportedly some of the essential micronutrients in plants which aid in combating against salt stress. These trace elements upregulate stress-responsive genes associated with biosynthesis of compatible solutes like proline, polyamines, and enzymatic or nonenzymatic antioxidants. The cellular antioxidant machinery is thus efficiently reprogrammed to scavenge toxic molecules like ROS and methylglyoxal, which in their abundance cause detrimental cytotoxicity. Expression of exporter genes facilitates effective efflux of Na^+ ions from the cytoplasm. Trace elements thus reestablish the cellular homeostasis in plants during salt stress and promote survival even under suboptimal conditions

of action of such beneficial elements. Figure 16.1 shows the ameliorative effects of trace elements during salt stress in plants. Treatment of plants with micronutrients upregulates genes associated with the biosynthesis of compatible solutes like Pro, PAs, and multiple enzymatic and nonenzymatic antioxidants. As a result, toxic biomolecules like ROS and MG are efficiently scavenged. The treated plants exhibit reduced levels of malondialdehyde (MDA) and lipid peroxidation in cell membranes. Excess accumulated Na^+ ions are exported out of the cell due to upregulation of transporter and stress-associated osmotic stress-responsive genes. Thus, the plants effectively exhibit salt-tolerant phenotype.

16.3.1 Selenium

Selenium in cultivated soils is available in two prevalent forms, selenate and selenite, of which selenite exhibits higher toxicity in the system due to its faster incorporation and accumulation (Dhillon and Dhillon 2003). Though Se is a necessary micronutrient for the animal system, its essentiality in higher plants remains ambiguous. However, it might be crucial for endemic plants like Se hyperaccumulators, *Astragalus* and *Stanleya*, growing on seleniferous soils. Terry et al. (2000) showed that the beneficial effects of Se on such hyperaccumulators are reduced when the soil phosphate level is low. This indicates at a correlation between Se and phosphate nutrition where Se antagonizes phosphate toxicity in the Se hyperaccumulators. In Se non-accumulator plants like ryegrass, lettuce, potato, and buckwheat, Se exerts its beneficial effects at low concentrations (Hartikainen 2005). Trace concentration of Se promotes normal growth and development, whereas moderate concentration is required to maintain homeostatic functions (Kaur et al. 2016). Se is also necessary for the growth of algae like *Chlamydomonas reinhardtii*, as it is a structural component of selenoproteins and seleno-tRNAs (Lobanov et al. 2007).

Se reportedly protects plants against multiple abiotic stresses like salinity, drought, cold, high temperature, heavy metal toxicity, and UV-B irradiation by maintaining the ion balance and the cellular structural integrity. The antioxidative machinery is recharged by the redistribution of essential elements induced in the presence of Se (Feng et al. 2013). Se also regulates the electron transport complex (ETC) and thus increases the photosynthetic efficiency (Kaur et al. 2014). A pot experiment with three rice cultivars, BRRI dhan45, BRRI dhan47, and Nipponbare, grown under a gradient (50–150 mM) of salt concentrations showed reduced height of plants, number of tillers, relative water content in the leaves, and chlorophyll content in a dose-dependent fashion (Naim 2014). Exogenous treatment of the seedlings with 0.5 mM Na_2SeO_3 significantly recovered the plants from the deteriorative effects of stress. The cultivar-specific salt tolerance conferred by 0.5 mM Se was most prominent in the plants exposed to 50 mM salt stress, and the beneficial effects could be observed up to 100 mM NaCl concentration (Naim 2014). Mozafariyan et al. (2016) showed that the deleterious impacts of 25 mM and 50 mM NaCl stress on tomato plants could be alleviated by exogenous application of Se at very low concentrations (5 or 10 μM). A concentration of 10 μM Se increased the concentration of the photosynthetic pigments and elevated the activities of antioxidant enzymes like CAT. Application of 5 μM Se also reduced the ROS levels and increased plant performance under stress (Mozafariyan et al. 2016). Dual application of Se and silicon (Si) ameliorated the adverse effects imposed by 10 ds m^{-1} NaCl on the annual herb, *Anethum graveolens* (Shekari et al. 2015). Addition of 1.5 mM Na_2SiO_4 and 5 μM of selenate in the root medium increased the K^+/Na^+ ratio and the activities of SOD and CAT in the stressed plants. The treated plants exhibited improved ion balance and osmotic adjustments which generated salt tolerance (Shekari et al. 2015).

Recently, Habibi (2017) reported that application of Se at 1 mg L^{-1} enhanced the salt tolerance in parsley (*Petroselinum crispum*) plants. The treated plants showed improved quantum yield of photosystem II along with higher accumulation of carotenoids and conventional scavengers of ROS. Se reduced Na^+ levels in the shoot by limiting the root-to-shoot translocation and by promoting Na^+ exclusion from the cell sap. Se was also found to bind to Na^+ in the root cell wall (Habibi 2017). Exogenous application of 25 μM Na_2SeO_4 rejuvenated the entire antioxidant system in rapeseeds exposed to 100 and 200 mM of NaCl stress (Hasanuzzaman et al. 2011).

The treated plants exhibited higher scavenging of ROS, detoxification of MG, and lower accumulation of MDA. It was observed that the enhanced activities of antioxidant enzymes like APX, MDHAR, DHAR, GR, GST, GPX, CAT, and glyoxalase I and II (Gly I and Gly II) led to the lower peroxidation of membranes and hence reduced the production of MDA (Hasanuzzaman et al. 2011). Similar salt tolerance was observed in cucumber seedlings treated with 5 and 10 μM Se under salt stress of 50 mM (Hawrylak-Nowak 2009). The growth-promoting effects of Se were attributed to the antioxidative activity of the element itself, higher accumulation of Pro, and decrease in the content of Cl^- in the shoots. Increased biosynthesis of the photosynthetic pigments strengthened the metabolic balance to support growth even under salinity (Hawrylak-Nowak 2009). Application of Se at 1 μM concentration increased the net photosynthetic rate and alleviated the NaCl-induced damages in the chloroplast ultrastructure in *Zea mays*. The treated plants exposed to salt stress exhibited higher activities of SOD and APX, along with upregulation of *mitogen-activated protein kinase 5* (*ZmMPK5*), *ZmMPK7*, and *calcium-dependent protein kinase* (*ZmCPK11*). The Se-induced salt tolerance in maize was also due to efficient compartmentalization of Na^+ brought about by the upregulation of the membrane Na^+ exporter, *ZmNHX1*, in the roots (Jiang et al. 2017).

16.3.2 Silicon

Silicon has been correlated with generating salt tolerance in several agriculturally important crops like wheat, rice, maize, barley, sorghum, tomato, and soybean (Rizwan et al. 2015). Si is available to plants as monosilicic acid, $Si(OH)_4$ in the soil, and water. Within plants, it gets deposited in the cell walls as amorphous silica (SiO_2-nH_2O) and increases cell wall rigidity by interacting with pectins and polyphenols. Si^{4+} content has been found to be higher in monocotyledons compared to dicotyledons, and hence Si is often classified as a “quasi-essential” element for plants (Kaur et al. 2016). Due to deposition in the leaf cuticle and epidermal cells in the cell wall, Si lowers the transpiration rate and prevents desiccation of the plant during salt stress. Si has also positive role on seed germination under saline conditions. About 1 mM of nano-Si increased tomato germination under 50 mM NaCl, whereas 1–5 mM Si enhanced the germination rate, germination index, and vitality index of *Momordica charantia* under 50–100 mM salinity (Haghighi et al. 2012; Wang et al. 2010).

Application of Si in the diatomite form increased the fresh weight, dry weight, and photosynthetic efficiency of Egyptian clover (*Trifolium alexandrinum*) exposed to salt stress. The treated plants exhibited increased accumulation of Mg, K, P, and Ca (Abdalla 2011). The pod yield, number of seeds per plant, and chlorophyll content were increased in salt -stressed *Vicia faba* plants treated with Si (Kardoni et al. 2013). The seed weight and yield in Si-treated *Phaseolus vulgaris* plants increased under salt stress (Parande et al. 2013). Li et al. (2015) reported improved root morphology, total root length, surface area, total volume, and average diameter of salt-stressed tomatoes treated with Si. Application of K_2O_3Si increased plant weight, ear length, seed yield, and chlorophyll content in wheat plants exposed to salinity (Bybordi 2014). In similar experiments, it was observed that 1 mM Si could ameliorate the toxic 120 mM NaCl stress in wheat seedlings (Chen et al. 2014). The overall ameliorative effects of Si in plants exposed to salinity were also observed in rice, canola, and the halophytic grass, *Spartina densiflora* (Gurmani et al. 2013a, b; Hashemi et al. 2010; Mateos-Naranjo et al. 2013). Habibi et al. (2014) reported an increase in the water use efficiency (WUE) in Si-treated pistachio (*Pistacia vera*) plants grown on saline media. In another study, salt-stressed maize plants treated with Si exhibited increased photosynthetic rate, stomatal conductance, and intercellular CO_2 concentration (Xie et al. 2015). Zhu et al. (2015) showed that 0.3 mM Si can improve salt tolerance in cucumber seedlings by enhancing water uptake through roots and upregulation of genes encoding aquaporins to facilitate water influx. Similarly, Liu et al. (2015) showed that Si-treated sorghum plants exhibit upregulated expression of aquaporin channel encoding *PIP* genes.

Si application increased the Ca content in the shoots of cucumber, cowpea, and kidney bean plants growing on saline media (Khoshgoftarmanesh et al. 2014). The N, P, K, and Ca content in the shoots and seeds of salt-stressed faba beans also increased upon treatment with Si (Hellal et al. 2012). Si-treated canola plants maintained high P and Fe levels even under saline conditions (Farshidi et al. 2012). Si application triggered higher accumulation of P, K, Ca, and Mg in stressed *Moringa oleifera* compared to the non-treated stressed plants (Hussein and Abou-Baker 2014). Xu et al. (2015) showed that Si treatment changed the entire mineral distribution in the root tips and leaf blades of *Aloe* plants exposed to salinity.

Si mitigates salt tolerance even by inducing the accumulation of compatible solutes and adjusting the levels of stress-responsive phytohormones like ABA, salicylic acid (SA), jasmonic acid (JA), indole acetic acid (IAA), etc. (Fahad et al. 2015). Foliar treatment of Si in okra plants growing under saline conditions led to increased photosynthetic rate, stomatal conductance, transpiration rate, WUE, and number and size of stomata. High accumulation of Pro, GB, and total free amino acids in both shoots and roots along with decreased lipid peroxidation and enhanced activities of SOD, CAT, and GuPX was observed in the treated plants (Abbas et al. 2015). However, Si application reduced the Pro content in tobacco, soybean, maize, and turfgrass during salt stress (Rizwan et al. 2015). Treated canola plants exhibited higher lignin content under salt stress (Hashemi et al. 2010). Levels of sucrose, fructose, and PAs increased in salt-stressed sorghum, whereas the ethylene content decreased after exogenous spraying of Si (Yin et al. 2016). Si improved salt tolerance in sorghum by regulating essential metabolic processes rather than merely acting as a mechanical barrier. Exogenous spermidine treatment exhibited similar ameliorative effects as with Si, whereas exogenous application of PA inhibitor, dicyclohexylammonium sulfate (DCHA), eliminated Si-mediated salt tolerance in sorghum (Yin et al. 2016). Wang et al. (2015) showed that 0.83 mM Si enhanced salt tolerance in cucumber by increasing Na^+ efflux in the leaves and by maintaining high levels of both free and conjugated types of PAs.

Kim et al. (2014) showed a correlation between temporal variations in the levels of JA and SA with the duration of Si exposure to salt-stressed rice seedlings. Short-term

(6 and 12 h) Si treatment in rice reduced the JA levels, while the SA levels fluctuated irregularly. The ABA-biosynthesis genes like *zeaxanthin epoxidase* (*ZEP*) and *9-cis-epoxycarotenoid dioxygenase 1* and *4* (*NCED1*, *4*) were upregulated after 6–12 h of Si exposure. The genes were downregulated after 24 h of Si treatment (Kim et al. 2014). Lee et al. (2010) showed that Si treatment in soybean seedlings growing under saline conditions decreased the ABA levels and increased the content of the germination-promoting hormone, gibberellic acid (GA). Liang et al. (2015) reported higher ethylene emission in salt-stressed tobacco seedlings treated with Si due to increased transcription of the ethylene biosynthetic genes.

Si triggered the activities of APX, CAT, and GuPX in the alfalfa seedlings exposed to salinity (Wang et al. 2011). The antioxidant machinery was found to be recharged in Si-treated tomato plants grown both in sand culture and saline solution culture (Li et al. 2015; Muneer and Jeong 2015). Improved cytochrome *b6f* and ATP synthase activity was observed in the leaf chloroplasts after treating the salt-stressed tomato seedlings with Si (Muneer et al. 2014). Several salinity-associated genes encoding dehydration-responsive element-binding protein 1, 2, 3 (DREB1, 2, 3), APX, SOD, and CAT and the genes involved in Si transport like *leLsi-1*, *-2*, and *-3* were found to be upregulated in the salt-stressed tomato seedlings (Muneer and Jeong 2015). Si dosage reduced lipid peroxidation, electrolyte leakage, and H_2O_2 content in pea plants exposed to salinity (Shahid et al. 2015). Wheat plants treated with 150 mg L^{-1} Si showed increased SOD and CAT activities and decreased GuPX activity and electrolyte leakage (Ali et al. 2012). Ali et al. (2013) reported that application of 2 mM Si increased the enzymatic activities of SOD, GuPX, and CAT along with the accumulation of AsA and GSH in the sunflower seedlings exposed to salt stress. Field experiments in salt-stressed sorghum showed that Si dosage triggered the activities of SOD, GuPX, CAT, APX, and GST (Kafi et al. 2011). Similar antioxidant effects of Si during salinity have been reported in lettuce, spinach, barley, grapevine, and *Ajuga multiflora* (Rizwan et al. 2015). In spite of several positive correlations between Si and salt tolerance, the exact molecular mechanism is still unclear. Further investigations focusing on the transcriptomic and proteomic avenues in this field are required.

16.3.3 Zinc

Zinc in trace quantities acts as a growth-promoting agent for plants growing under saline conditions. Studies indicate that a moderate Zn concentration of 1 mmol L^{-1} and 1% NaCl acted synergistically to yield a high final biomass in *Spartina densiflora* seedlings (Redondo-Gomez et al. 2011). Iqbal and Aslam (1999) showed that Zn supplementation promoted salt tolerance in rice seedlings. The treated plants had higher tiller height, dry weight, and fresh weight under 70 mM NaCl stress. Recently, Jan et al. (2017) reported that Zn treatment significantly minimized oxidative stress and promoted root, shoot, and spikelet growth in salt-stressed wheat plants. The levels of photosynthetic pigments, Pro, total phenolics, and total carbohydrates were higher in the treated plants compared to the untreated seedlings under stress. While Zn counteracted the adverse effects of salinity, it also triggered high activities of SOD, CAT, and APX. The study showed that K and Zn acted synergistically to counteract salt stress in the wheat seedlings (Jan et al. 2017).

16.3.4 Manganese

Manganese is an essential cofactor of the antioxidant system. It is required for the activation of Mn-SOD, Mn-CAT, etc. It is also assumed that Mn itself acts as a scavenger of ROS. Pandya et al. (2004) reported that exogenous Mn improved relative growth rate, net assimilation rate, and photosynthetic efficiency in the salt-stressed barley plants. Sebastian and Prasad (2015) showed reduced lipid peroxidation and improved biomass, chlorophyll, and carotenoid content in Mn-treated plants. In a recent study, it was observed that 0.5 mM Mn could ameliorate 150 mM NaCl stress in 12-day-old rice seedlings (Rahman et al. 2016c). The treated plants recovered from chlorosis and showed improved ionic and osmotic homeostasis even under high saline conditions. Salt tolerance was mainly due to effective scavenging of ROS, MG detoxification, and efficient accumulation of AsA, phenolics, and flavonoids. Activities of antioxidant enzymes like MDHAR, DHAR, SOD, and CAT were also high in the Mn-treated plants (Rahman et al. 2016c).

16.3.5 Iron

Iron is an essential micronutrient necessary for multiple physiological developments in plants. Recently, Yasmeen et al. (2016) designed Fe nanoparticles (Fe NPs) to study their effects on the salt-tolerant wheat variety, NARC-11. It was observed that the Fe nanoparticles (NPs) stimulated the production of proteins associated with the photosynthetic and metabolic machineries. The ribulose bisphosphate carboxylase/oxygenase (RuBisCo) activity increased three times in the Fe NP-treated plants compared to the untreated ones (Yasmeen et al. 2016). In an interesting study, Fe deficiency in the rice cultivar, Dongdao-4, was correlated with salt tolerance. The Dongdao-4 plants grown in saline-alkaline medium was found to develop better than the other cultivar, Jigeng-88, due to higher expression of Fe deficiency-responsive genes like *IRO2*, *iron-regulated transporter 1* (*IRT1*), *nicotianamine synthase 1* (*NAS1*), *NAS2*, *yellow strip-like 2* (*YSL2*), and *YSL15*. This resulted in high Fe content in the roots and shoots of Dongdao-4 which was responsible for conferring saline-alkaline tolerance (Li et al. 2016).

16.3.6 Boron

Though B is phytotoxic at high concentration, trace amounts of this micronutrient is beneficial for crops. Soil application with moderate amounts of B (1.5 Kg B ha^{-1}) conferred salt tolerance in rice plants grown on saline and saline-sodic soils. The plants had higher yield and reduced Na^+ and Cl^- content in their shoots. However, a higher concentration of 6 Kg ha^{-1} severely hampered seedling growth and straw production under saline and saline-sodic conditions (Mehmood et al. 2009).

16.3.7 Iodine

Iodine is not an essential micronutrient for land plants. However, it can regulate critical antioxidant responses in some aquatic plants. The function of I in scavenging ROS and inducing SOD, APX, and CAT activities in plants has been established (Medrano-Macias et al. 2016). Such increased levels of antioxidants promote better adaptability in plants to tackle stress conditions. Leyva et al. (2011) reported that exogenous application of I conferred salt tolerance in the lettuce plants exposed to saline conditions.

16.4 Conclusion and Future Perspectives

In this chapter, we have discussed about a variety of micronutrients which are beneficial for plant physiological development under saline conditions. Though plants have well-organized antioxidant machinery, the sensitive varieties lack the strong induction to trigger this protective system when they are exposed to abiotic stresses. Micronutrients applied in trace amounts act as supplements which recharge and reprogram the antioxidant system and lead to the osmotic balance. This aids in plant sustainability and viability even under suboptimal conditions like salt stress.

The intricate mechanisms by which the trace elements mediate salt tolerance are intriguing and interesting but are not completely known. This field lacks investigations at the molecular and epigenomic levels. Furthermore, though the technology is economic and easy, proper optimization is absolutely essential to avoid unnecessary crop losses. In this regard, exhaustive experimentations should be executed to identify the exact dose, duration, and application procedure in species – as well as cultivar-specific manner.

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Chapter 17
Nutrient Homeostasis and Salt Stress Tolerance

Shahid Farooq, Shakeel Ahmad, Sajjad Hussain, and Mubshar Hussain

Abstract Soil salinity is an unavoidable constraint in crop production globally. Soil salinization is often caused by improper soil management and/or crop production practices, which has made highly productive lands barren/unusable. Plant species have evolved several mechanisms to cope with salinity stress. Nutrient homeostasis is among the different mechanisms employed by plant species to withstand elevated salt levels in the root zone. Nutrients are the mediators of metabolism, so their cytoplasmic levels need to be effusively controlled both under stressful and benign environments. Several studies report the homeostasis of a single ion, i.e., sodium, potassium, or chloride. However, limited studies are available reporting the role of nutrient homeostasis (all nutrients together) under salinity stress. This chapter describes the role of nutrient homeostasis and ion channels and transporters in salt stress tolerance of plant species. The ion efflux at plasma membrane and vacuolar compartmentation in response to salinity stress has been described in detail. The impaired uptake of the nutrients is an obvious effect of salinity, mainly disturbing the sodium and potassium uptake. Much of the research has been done to test the role of different nutrients on salinity alleviation, and silicon is found to alleviate the negative effects of salinity. The nutrient homeostasis starts from ion sensing, uptake, transport, and activation of defense mechanisms as well as regulation of genes or gene networks to alleviate/withstand the adverse effects of salinity. Thus, the ion sensing, uptake, transport, and gene defense activation in response to salinity stress have also been described comprehensively.

Keywords Nutrient homeostasis · Plants · Salinity stress · Ion channels · Ion efflux

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17.1 Introduction

Soil and water salinity stresses are unavoidable globally as around 830–950 million hectares of global soils are estimated to be affected by salinity (Rengasamy 2006, 2010; Ruan et al. 2010; Teakle and Tyerman 2010). Nearly half of the salt-affected soils are sodic, where 15% of cation exchange capacity is contributed by Na^+ (Brady and Weil 2008; Rozema and Flowers 2008). The chloride (Cl^-), sulfate (SO_4^{2-}), carbonates (CO_3^{2-}), and bicarbonates (HCO_3^-) salts of different metals such as sodium (Na^+), potassium (K^+), magnesium (Mg^+), and calcium (Ca^{2+}) may give rise to soil salinity; however, sodium chloride (NaCl) is the most prevalent cause of salinity globally (Rengasamy 2002; Yadav et al. 2011).

Soil salinization is caused by improper management practices, which has made highly productive lands barren/unusable. The Mesopotamia, different regions of Indian and Pakistani Punjab, and the Fubei region in China are some of the examples of the areas where salinity has rendered productive lands barren (Hillel 2000, 2005; Swarajyalakshmi et al. 2003; Wang et al. 2008). The salts from deep in groundwater are moved upward by cultivation practices (Rengasamy 2006; Brady and Weil 2008; Yadav et al. 2011). The increased consumption of water by human has made salinity more acute today than before (Epstein and Bloom 2005; Brady and Weil 2008; Rozema and Flowers 2008). Out of the total available water for human consumption, 70% is consumed by agriculture, and this amount is rising with escalating population pressure (Hightower and Pierce 2008).

The noteworthy challenge for global agriculture is the production of an extra 70% food crops for another 2.3 billion people worldwide by the year 2050 (FAO 2009). However, the increased food demand is constrained by salinity. Over 20% of arable land around the world is influenced by salt stress, and the area is expanding steadily with each passing day. The crop plants could be divided into two major groups on the basis of their adaptive response to elevated salt levels in the soil. The first group comprises of the plants which can withstand salinity, known as halophytes (Hasanuzzaman et al. 2014), whereas the second group consists of the crop plants which are unable to tolerate the elevated salt levels and die, termed as glycophytes. Thus, salinity is regarded among the most ruthless abiotic stresses, which severely hamper the productivity of arable crops globally (Flowers 2004; Munns and Tester 2008).

Numerous physiological and metabolic processes are significantly altered by salinity stress. The extent of change in these processes depends on the nature of salts and the level and duration of stress, eventually hampering crop production (James et al. 2011; Rahnama et al. 2010; Munns 2005; Rozema and Flowers 2010). Salinity stress creates osmotic stress, which impair plant growths at the initial phases that is followed by ion toxicity at the later stages. Both osmotic stress and ion toxicity create unfavorable conditions for the normal growth and development of crop plants (James et al. 2011; Rahnama et al. 2010). High accumulation of salts at the initial phases of plant growth decreases the water absorption capacity of roots. Similarly, the osmotic stress caused by salinity stress increases water loss form the leaves. Thus salinity stress is also termed as hyperosmotic stress due to these reasons (Munns 2005).

Osmotic stress caused by elevated salt levels induces numerous physiological changes in crop plants. These physiological changes include membrane disruption, nutrient imbalance, lower detoxification of reactive oxygen species (ROS), diminished photosynthesis, opening of stomata, etc. (Munns and Tester 2005; Rahnama et al. 2010). Since NaCl is the most prevalent cause of salinity, accumulation of Na^+ and Cl^- ions in plant tissues is the most devastating effect on the crop plants exposed to elevated NaCl concentration in the soil. The K^+ is a necessary element for normal plant growth; however, elevated levels of Na^+ disrupt its uptake. The Na^+-induced reduction in K^+ uptake results in disturbed plant growth, low productivity, and even mortality based on the adaptive response of the crop plants to elevated salt levels in the soil (James et al. 2011). The ROS, such as singlet oxygen, superoxide, hydroxyl radical, and hydrogen peroxide, are produced in excess when plants are exposed to salinity stress (Apel and Hirt 2004; Mahajan and Tuteja 2005; Ahmad 2010; Ahmad et al. 2012; Ahmad and Umar 2011). Salinity-induced overproduction of ROS affects various cellular components (i.e., lipids, proteins, and DNA) through oxidative damage. Salinity induced oxidative damage eventually interrupts numerous functions at cell level in crop plants.

The physiology, development, and cellular metabolism in plants are driven by nutrient homeostasis (Clemens et al. 2002; Amtmann and Blatt 2009). The synthesis of organic macromolecules requires nutrient elements, which complete various functions in the key proteins. Moreover, they also act as cofactor of enzymes or as signaling molecules. The daily fluctuations posed by the environment on the plants have dramatic effects on the physiology and metabolism. The environmental fluctuations cause recurring fluctuations in the demands of essential nutrients required for the photosynthesis in chloroplasts. Moreover, nutrient transport pathways in xylem are also altered by the rhythmic changes in transpiration rates. Hence, continuous nutrient mobilization is required among organelles and tissues, particularly under nutrient deficit environments.

The identification of Na^+ transport was a key gap in understanding the ionic homeostasis in plants under salinity stress (Niu et al. 1995). Generally, living cell under low or high salinity tend to balance passive Na^+ inclusion with Na^+ exclusion at two different levels. The balance is required at the plasma membrane and back to the apoplast, or across the tonoplast into the vacuole. Time is an imperative aspect needing consideration for salinity tolerance in addition to the considerable energy required for Na^+ flow, as the Na^+ uptake rate determines the rate at which Na^+ reaches toxic levels within the cell. Although there are number of studies available dealing with salinity tolerance and nutrient homeostasis under salinity stress, only a few aspects of nutrient homeostasis has been addressed. In this chapter, we will discuss all aspects of nutrient homeostasis and salinity tolerance in plant species. In summary, the chapter provides detailed information about how nutrients are mobilized under salinity stress to maintain normal growth.

17.2 Role of Nutrient Homeostasis in Salt Tolerance

Nutrients are the mediators of metabolism, so their cytoplasmic levels need to be effusively controlled both under stressful and benign environments. The reestablishment of nutrient homeostasis under stressful environments is the key strategy of plant species to improve their resistance against abiotic stresses, particularly salinity. Both types of nutrient homeostasis, i.e., ionic and osmotic homeostasis, need to be restored for salinity tolerance. The ionic homeostasis is determined/mediated by various ion transporters. Two nutrients, i.e., Na^+ and Cl^-, are the most detrimental to plant health under salinity stress; therefore both need to be under control in order to withstand higher salt levels (particular of NaCl) in growth medium. Many enzyme activities are inhibited by elevated levels of Na^+, therefore Na^+ accumulation in the cytoplasm or in organelles other than the vacuole needs to be prevented to reach at higher levels. This can be accomplished by either preventing Na^+ entry or reducing it to safe or lower levels. The Na^+ entry into plant cells is known to be controlled by nonselective cation channels (NCC) (Amtmann and Sanders 1998). The NCC is a channel, independent of voltage and serves as Na^+ entry gate into the plant cells. Furthermore, there is the K^+ outward-rectifying channel, opened by depolarization of plasma membrane and enables K^+ exclusion and Na^+ entry, which leads to the accumulation of Na^+ in cytosol. The excess Na^+ is pushed into vacuole with the help of vacuolar Na^+/H^+ exchanger. Another pump, the H^+/Ca^{2+} antiporter, also aids toward Ca^{2+} homeostasis (Zhu 2002; Mahajan et al. 2006).

Na^+ homeostasis is imbalanced by high salinity, while collective action of numerous pumps, ions, Ca^{2+} sensors, and their downstream interacting partners tends to normalize it. The organized action of these pumps, ions, and Ca^{2+} sensors ultimately causes efflux of excess Na^+ ions. Certain channels tend to exhibit higher K^+ sensitivity/selection over Na^+, and K inward-rectifying channel is one of them. The excessive NaCl hyperpolarizes the plasma membrane, thus K-rectifying channel mediates K^+ influx in response to higher NaCl, thus results in selective accumulation of K^+ over Na^+. On the other hand, there are some channels restrict the Na^+ influx into the cytosol rather than selective accumulation of K^+ over Na^+. The histidine kinase transporter (HKT) is such an ion transporter, which restricts Na^+ entry into the cytosol (Platten et al. 2006). There are numerous voltage-dependent anions, which are upregulated in response to elevated salinity, thus normalizing the Na^+ homeostasis. The upregulation of a voltage-dependent anion has been observed in *Pennisetum glaucum* under salinity stress (Desai et al. 2006).

The Ca^{2+} has a significant role in salinity tolerance of crop plants by keeping the pivotal role in nutrient signaling under elevated salt levels. The cytosolic Ca^{2+} is increased under salinity stress, which initiates stress signal transduction pathways for tolerance to increased salinity levels. In addition, Ca^{2+} binding proteins may deliver an extra regulation level of Ca^{2+} signaling. The information provided by Ca^{2+} signaling is recognized and decoded by sensor proteins, which communicate this information to start a phosphorylation cascade regulating gene expressions.

Any Na^+ entering the cells can be stored in the vacuole or transferred outside the cell. Na^+ compartmentation is an inexpensive way to prevent Na^+ toxicity in the cytoplasm, as Na^+ can be used as a vacuolar osmolyte to provide osmotic homeostasis. Many salt-tolerant plants (halophytes) use this strategy to withstand the negative effects of salinity stress (Flowers et al. 1977).

The nutrient homeostasis prevents the Na^+ entry into the cell, reduces it or pushes the excess Na^+ into the vacuoles. There are a lot of channels and transporters involved in this process, which ultimately reduce the brutal effects of Na^+ on plant growth. The most commonly observed homeostasis is for K^+ and Ca^{2+} ions, which mitigate the adverse effects of Na^+. The channels and transporters involved will be discussed in the coming sections. It can be briefly concluded that nutrient homeostasis is inevitable to achieve salinity tolerance for plants, which is accomplished by several ways as described under.

17.3 Types of Homeostasis

The homeostasis in plant species under salinity stress is divided into two categories, i.e., osmotic and ionic homeostasis. The osmotic homeostasis comprises of accumulation of compatible solutes, while ionic homeostasis consists of ionic influx and efflux and compartmentation at different levels in plant cells. Since the scope of the chapter is nutrient homeostasis, we will only discuss osmotic homeostasis in this chapter.

17.3.1 Ionic Homeostasis and Salt Tolerance

The maintenance of ionic homeostasis by partitioning and absorption of ions is not only required for the normal growth of plants under salinity-free conditions but also for highly saline environments (Niu et al. 1995; Serrano et al. 1999; Hasegawa 2013). Both glycophytes and halophytes species are unable to tolerate elevated salt levels in the cytoplasm. Therefore, the extra salt is elated to vacuole or reserved in old tissues, which are then for protection against salinity stress (Reddy et al. 1992; Zhu 2003). The main salt in the soil is NaCl, so this chapter focused on the transport mechanism and Na^+ and its compartmentation.

The Na^+/H^+ antiporter transport the excess Na^+ entering to the vacuole. There are two different kinds of H^+ pump in the vacuolar membrane, i.e., H^+-ATPase (V-ATPase) type vacuole and vacuolar pyrophosphatase (V-PPase) (Dietz et al. 2001; Otoch et al. 2001; Wang et al. 2001). Among these two pumps, V-ATPase dominates plant cells. These pumps have a vital role in the preservation of solute homeostasis, ensure secondary transfer energy, and facilitate vesicle fusion in stress-free conditions. The viability of the plant species under stress conditions is dependent on V-ATPase activity (Dietz et al. 2001). It has been observed that the efficacy of the VATPaz pump was increased in hypocotyls of *Vigna unguiculata* when exposed to elevated salt levels (Otoch et al. 2001). However, V-PPase activity was retarded under same conditions. The activity of V-ATPase was increased in halophytic species *Suaeda salsa*, while V-PPase had a negligible role (Wang et al. 2001).

The role of "Salt Overly Sensitive" (SOS) stress signaling pathway has increasingly been suggested in ionic homeostasis as well as tolerance to elevated salinity (Hasegawa et al. 2000; Sanders 2000). The SOS signaling pathway includes three main proteins, which are SOS1, SOS2, and SOS3. The first protein, i.e., SOS1, encodes the Na^+/H^+ antiporter of plasma membrane and is vital for the regulation of Na^+ flux at the cellular level. At the same time, the Na^+ transport from roots to the shoot is eased by this protein; thus overexpression of the protein imparts tolerance to the crop plants against elevated salt levels (Shi et al. 2000, 2002). The second protein, i.e., SOS2, encrypts a serine/threonine kinase and is activated by the Ca^{2+} signals resulting from salinity stress. This protein comprises of well-developed N-terminal catalytic domain and a C-terminal regulatory domain (Liu et al. 2000). The third protein, i.e., SOS3, is a myristoylated protein that binds Ca^{2+} and contains a myristoylation site in its N-terminus. This site has an important role in imparting tolerance to crop plants against elevated salinity (Ishitani et al. 2000). Therefore, a strong increase in intracellular Ca^{2+} level is observed with increasing Na^+ concentration, which eases the binding with SOS3 protein. Intracellular Na^+ homeostasis is moderated by Ca^{2+} along with SOS proteins. The SOS2 protein is activated by SOS3 protein thus releasing the spontaneous inhibition. The SOS3-SOS2 complex is then laden onto the plasma membrane, where SOS1 is phosphorylated.

Phosphorylated SOS1 increases Na^+ flux, thus reducing the toxicity of Na^+ (Martınez-Atienza et al. 2007). Many plant species have established an effective method to maintain ion concentration at a low level in the cytoplasm. Membranes, together with their associated apparatuses, regulate the uptake and transport of ions under elevated salinity, thus play an essential role in maintaining the ions concentration of in the cytosol in response to increased salt levels (Sairam and Tyagi 2004). Different carrier and proteins, antiporters, and symporters carry out the transplantation phenomenon.

The maintenance of cellular Na^+/K^+ homeostasis is vital for plant survival under highly saline conditions. Ma et al. (2011) reported that *Arabidopsis* NADPH oxidases function under salt stress in the ROS-dependent regulation of Na^+/K^+ homeostasis in *Arabidopsis* by *AtrbohD* and *AtrbohF* genes. Plants maintain high K^+ level in cytoplasm (approximately 100 mM) for cytoplasmic enzyme activities. The K^+ concentration in the vacuole ranges from 10 to 200 mM. The vacuole is the largest K^+ pool within the plant cell. K^+ has a vital role in maintaining the turgor within the cell. The K^+ transporter and membrane channels transport K^+ to the plant cells against the concentration. The K^+ intake mechanism is strongly mediated by its amount present in the soil. When extracellular concentration of K^+ is low, high affinity K^+ carriers uptake K^+ from the soil. However, the low affinity K^+ channels get activated for restricted uptake when extracellular concentration of K^+ is high. On the other hand, a very low Na^+ ion concentration is maintained in the cytosol. Since both K^+ and Na^+ share the same transport mechanism, Na^+ competes K^+ for the carrier, under salinity stress due to the increased Na^+ concentration in the soil, thus reducing K^+ absorption (Sairam and Tyagi 2004; Munns and Tester 2008).

Numerous genes and proteins encoding K^+ carriers and channels such as Na^+ influx transporter (HKT) and the tonoplast Na^+/H^+ antiporter (NHX) have been recognized and duplicated in several crop plants. The expression of low abundance transcripts increases the uptake of K^+ under salinity stress. This expression of low abundance transcripts has been recorded in a halophyte species, i.e., *Mesembryanthemum crystallinum* (Yen et al. 2000).

The HKT family transporters found on the plasma membrane have a significant role in salinity tolerance through the regulating the transport of Na^+ and K^+. HKT Class 1 (HKT1) transporters, classified in *Arabidopsis*, prevent excessive buildup of Na^+ in leaves, thus protecting plants form the adverse effects of salinity stress. The HKT1 rice transporter removed extra Na^+ from xylem, thus protecting the photosynthetic tissue of the rice leaves from the Na^+ toxicity (Schroeder et al. 2013). Barragán et al. (2012) indicated that two localized tonoplast NHX proteins (NHX1 and NHX2) are vital for active K^+ uptake at the tonoplast. These proteins are required for regulation of turgor regulation and normal functioning of stomata. Several NHX isoforms have been proved to play an imperative role in ionic homeostasis (Na^+, K^+, H^+) in different crop species (Gálvez et al. 2012).

17.4 Cation Uptake, Mechanisms, Transporters Involved, and Role of Ion Channels

Crop plants grown under elevated salt levels are exposed to explicit ionic effects, which damage the enzymes structure as well as some macromolecules including Na^+ and Cl^-. The ionic effects also exert damages to the cell organelles as well as resulted in impaired photosynthesis and respiration. Salinity stress also results in the physiological drought resulting in impaired uptake and transport of nutrients. The disturbed uptake and transport of nutrients leads to imbalanced nutrition in crop plants under elevated salt levels (Munns and Tester 2008; Ruiz-Lozano et al. 2012). Higher accumulation and degradation of Na^+ and reduced K^+ uptake are the obvious detrimental effects of elevated salt levels on plant growth, while these mechanisms are still unclear or understudied (Chen et al. 2007). Na^+ is an important cation prevailing in the soils affected by salinity. The K^+ and Na^+ activate and inhibit numerous cytosolic enzymes, respectively (Shi et al. 2002). Under natural physiological circumstances, the plants hold 1–10 mM Na^+ and 60–100 mM K^+ in the cytosol (Bassil et al. 2012).

The Na^+ is a cytotoxin which severely disrupts proteins and membranes. Moreover, several physiological processes including cell expansion and cell division, metabolism (primary and secondary) and Na^+ severely impacts nutrient homeostasis

(Hasegawa et al. 2000; White and Broadley 2001; Munns and Tester 2008; Teakle and Tyerman 2010). The presence of excessive Na^+ in the soil restricts K^+, which decreases intracellular K^+ ultimately disturbing K^+/Na^+ imbalance (Hauser and Horie 2010; Leidi et al. 2010; Alemán et al. 2011; Pardo and Rubio 2011). Excessive presence of Na^+ offers strong competition to K^+ for even in the presence of high-affinity K^+ transport systems (Rus et al. 2004; Kronzucker et al. 2008; Alemán et al. 2009, 2011; Pardo and Rubio 2011). The conductance of K^+ is reduced by Na^+ through AKT1 (Qi and Spalding 2004) which suppresses the expression of *AtHAK5* (Nieves-Cordones et al. 2008; Alemán et al. 2011; Pardo and Rubio 2011).

The synthesis of proteins and activities of cytosolic enzymes are inhibited under abnormally high cytosolic Na^+/K^+ ratio (Shabala and Cuin 2008). Thus, plants are equipped with numerous mechanisms (biochemical and molecular) to withstand the brutal impacts of salt stress. Regulating salinity uptake genes and Na^+ and/or K^+ transport or compartmentation are the mechanisms developed by plants for adequate ionic homeostasis. The undue Na^+ accrual in cytosol is prohibited through a number of mechanisms by glycophyte plant species. The first mechanism is the selective uptake of ions to restrict Na^+ for the regulation of ionic homeostasis under salinity stress. The second mechanism is to maximize the Na^+ efflux to growth medium or to apoplastic spaces. The plant species finally can impound Na^+ into vacuoles for restricting the Na^+ transfer to the shoot (Cuin et al. 2011). The two mechanisms described above are vital and usually used by crop plants to control undue Na^+ buildup (Cuin et al. 2011; Cabot et al. 2014). The vacuolar Na^+ and K^+/H^+ antiporters NHXs catalyze the impounding of Na^+ into vacuoles (Cuin et al. 2011). Four different genes (*OsNHX1–4*) relating to these antiporters have recently been identified in rice crop (Fukuda et al. 2011; Kumar et al. 2013).

Plasma membrane Na^+/H^+ antiporter (SOS1) catalyzes the Na^+ efflux from cytosol to the growth medium or to apoplastic spaces in numerous crop plants (Kumar et al. 2013). The SOS1 is preferentially expressed in the cells which surround xylem, thus suggesting that this transporter plays a vital role in the redistribution of Na^+ between roots and shoots. The transporter has also been suggested to have ability of preventing Na^+ to reach the photosynthetic tissues (Shi et al. 2002; Olias et al. 2009). The unloading of Na^+ from photosynthetic organs and its recirculation to roots have also suggested as a mechanism imparting salinity tolerance to crop plants (Davenport et al. 2007). The high-affinity HKT transporters are reported to be involved in this mechanism from several crop plants (Garciadeblás et al. 2003; Ren et al. 2005).

Different studies relating to physiological and molecular mechanisms/processes have identified the channels and transporters involved in the tolerance mechanisms to elevated salt levels in various plant species. These channels and transporters are the passages for the ions required for cellular function related to ionic toxicity.

It is now known that HKT1 transporter-mediated salinity tolerance is too much complex than expected. To infer the role of these transporters, Chen et al. (2017) evaluated the correlation between the activity of two Mg^{2+} transporter, i.e., OsMGT1 and OsHKT1. It was observed that OsMGT1 mutants accumulated excessive amount of Na^+ with OsHKT1 mutants. The expression of OsMGT1 different plant parts such as parenchyma cells in xylem and phloem and leaf sheath tissue spatially overlapped with the expressions OsHKT1 (Kobayashi et al. 2017). These findings regarding the co-expression of these transporters added valuable information toward understanding complex Na^+ regulation mechanisms at the organismal level. The recent findings of Kobayashi et al. (2017) and Chen et al. (2017) cleared that nodes and sheaths have an imperative role in avoiding ion toxicity in the reproductive organs of plant species. The restricted transport of Na^+ to older leaves is a typical mechanism of salinity tolerance in plants (Cotsaftis et al. 2012); however, this mechanism vanished in OsMGT1 mutants (Chen et al. 2017). These findings suggest that the fine-tuning of HKT1 activity is mediated by OsMGT1 mutants. Thus, it is noteworthy to determine the cell-specific expression and functions/roles of OsMGT1 mutant at later stages, particularly reproductive development of the crop plants. The OsHKT1 is overexpressed during reproductive developmental stage of crop plants, particularly in node I (Kobayashi et al. 2017). It is obvious from the abovementioned both studies (Chen et al. 2017; Kobayashi et al. 2017) that nodes function as fences where OsMGT1 regulates the gating of OsHKT1 in a spatiotemporal manner to limit the ion toxicity.

Different cation channels which are nonselective (NSCC) are indulged in the unidirectional intracellular Na^+ influx. The members of NSCC, including HAK/KUP/KT and AKT1, are the channels having higher affinity for K^+ acquisition, whereas the low-affinity acquisition is mediated by different cation transporters including cation-Cl^- cotransporter and high-affinity K^+ transporter (HKT1 and HKT2) (Plett and Møller 2010; Zhang et al. 2010; Kronzucker and Britto 2011). Although NSCCs and HKT1 transporters are main mediators of Na^+ uptake, their comparative contribution is ambiguous (Roberts and Tester 1997; Amtmann and Sanders 1998; Demidchik and Maathuis 2007). Among two classes of HKT proteins, HKT1 is more selective for Na^+, while HKT2 proteins exhibit higher K^+ selectivity than Na^+ or remain nonselective (Hauser and Horie 2010; Lan et al. 2010; Mian et al. 2011). Ali et al. (2012) have recently identified a HKT1 family transporter having higher K^+ selectivity than Na^+ from *Thellungiella sp*. The SOS1 Na^+/H^+ antiporter controls the Na^+ efflux across the plasma membrane. The antiporter has phylogenetic similarity with mammalian NHE and bacterial NhaP Na^+/H^+ antiporters (Zhu 2002, 2003; Pardo and Rubio 2011; Kronzucker and Britto 2011). The Na^+ efflux to the apoplast is mediated by SOS1 against the electrochemical potential by secondary active transport driven by the H^+ gradient across the plasma membrane.

17.5 Anion Uptake, Mechanisms, Transporters Involved, and Role of Ion Channels

The anions are more prevalent than cations in the soil; however, the transport mechanisms of anions are less understood than cation transport mechanisms both under normal soil conditions and elevated salt levels. The Cl^- transport mechanisms are also less discussed than cations for plant mineral nutrition as well. The Cl^- performs several mechanisms such as enzyme activities' regulation in cytoplasm acting as an important cofactor in photosynthesis and counteranion stabilizing membrane potential and also regulates turgor and pH. Thus it is considered as an important micronutrient for plant growth (Tyerman 1992; Marschner 1995; Teodoro et al. 1998; Xu et al. 1999; White and Broadley 2001). The higher amounts of Cl^- are toxic for crop plants. The critical toxicity level of Cl^- is known to be 4–7 and 15–50 mg g^{-1} dry weight for Cl^--sensitive and Cl^--tolerant species, respectively (Xu et al. 2000). The most dominant ions in NaCl-affected soils are Na^+ and Cl^-, which at higher concentrations are toxic for plant species. However, some of the plant species are able to better tolerate Na^+ transport than Cl^-, while others have better control on Cl^- transport (Munns and Tester 2008). The differential salt tolerance level of plant species has strong correlation with Cl^- transport and exclusion from shoots. Different legume species such as *Trifolium pratense* (Winter 1982; Rogers et al. 1997), *Medicago sativa* (Sibole et al. 2003), *Glycine max* (Luo et al. 2005), and *Lotus* (Teakle et al. 2006, 2007) have higher tolerance level to salinity and thus can better exclude Cl^- than nonleguminous species. Similarly, some woody species, such as *Pinus banksiana* (Franklin and Zwiazek 2004), *Citrus reticulata*, and *Vitis vinifera* (Sykes 1992; Romero-Aranda et al. 1998; Moya et al. 2003), also have better control over Cl^- transport and exclusion.

The focus of research dealing with salinity tolerance has been to maintain favorable K^+/Na^+ ratio through establishing selectivity between Na^+ and K^+. Several specific transport systems, or combination of selective transporters at different membranes as well as different cells alongside the transport pathways through root to shoot, are related to Na^+ and K^+ selectivity (Hua et al. 2003; Horie et al. 2005; Volkov and Amtmann 2006; Apse and Blumwald 2007; Byrt et al. 2007). A resembling mechanism might be present for the exclusion or selectivity of Cl^- at least for major macronutrient anions (NO_3^-, SO_4^{2-}) and organic anions. However, the mechanisms and transporters mediating the Cl^- exclusion and or the pathways involved are not well-studied until now. Several micronutrients impart salinity tolerance to crop plants, which might be attributed to the activities of transporters and selective channels (Grattan and Grieve 1998). The NO_3^- is the most prevalent univalent anion in soils under salinity-free conditions; therefore it must be focused to understand Cl^- and salinity tolerance (Fricke et al. 1994; Frachisse et al. 1999). There are numerous anion channels having higher affinity and more selective to NO_3^- than Cl^- (Roberts 2006). Thus the NO_3^- in growth media could decrease the concentration of Cl^-concentration in (Abdolzadeh et al. 2008; Gimeno et al. 2009; Song et al. 2009). The NO_3^-/Cl^- balance is akin of K^+/Na^+ balance or interactions as well as selectivity for Cl^- efflux mechanisms.

Charge balance is another subject which has not been sufficiently addressed and correlated with the comparative roles of Cl^- and Na^+ in salinity tolerance. For salinity tolerance the movement and net charge must be in equiliburium by the opposite ions in each compartment to reach the similar charge in each section. If Cl^- uptake is higher, then a cation (e.g., Na^+) uptake or exclusion of anion must balance this charge from Cl^- perspective. The potential anions which could balance this charge are not readily moved out as these are related to nutrition (e.g., NO_3^-) or carbon balance (e.g., malate). However, from Na^+ viewpoint, addition to the opposite of abovementioned mechanisms, either Cl^- or K^+ might be excluded (Shabala et al. 2006). This exclusion is true in a sense if Na^+ substitutes K^+ role in vacuole and concentration of K^+ in the cytoplasm is retained below or equal to adequate limits (Carden et al. 2003). The voltage changes across the membrane eventually regulate charge balance, which then impacts the driving force on counterions, effectually as a self-regulating system. The type, nature, and selectivity of transporters present at the membrane barriers as well as their response to voltage changes in the membrane eventually determine the nature of the charge balance. These responses are also important for the energy needs of transport (Britto and Kronzucker 2009). Plett and Møller (2009) are referred for the further readings on Na^+ transport mechanisms.

Various aspects of anion transport have been covered in detail by several reviews (Roberts 2006; De Angeli et al. 2009). However, there has been lacking information on the Cl^- transport mechanisms and their role in salinity tolerance (White and Broadley 2001). Salinity tolerance of different plant species is imparted by a number of traits including osmotic stress tolerance, compatible solute accumulation, and tolerance to oxidative stress. Several reviews have described the traits imparting salinity tolerance in various crop species (Bartels and Sunkar 2005; Munns 2005; Flowers and Colmer 2008; Munns and Tester 2008). In summary, not only cation uptake and balance is essential for salinity tolerance, but anions also play an integral role. Thus studying the anion uptake mechanisms, regulation of anions, transporters, and channels involved in transport of anions should be the focus of salinity tolerance studies to be conducted in the future.

17.6 Ion Efflux at the Plasma Membrane

Maintenance of high tissue K^+/Na^+ ratio through regulating Na^+ uptake and transport in plant species has been interpreted in various studies for salinity tolerance. Thus, a high K^+/Na^+ has been considered as an important trait imparting salinity tolerance to crop plants (Shabala and Pottosin 2014). Since K^+ participates in various physiological processes; thus, this interpretation is logical. Moreover, higher concentration of Na^+ often competitively disrupts K^+ uptake, and increased K^+ deficiency under elevated salt levels severely impedes plant growth and development. Thus, it could be concluded that sensitivity of crop plants to salinity stress is because of K^+ deficiency, especially keeping in view that concentration of K^+ in soil is typically in the micromolar range (Very and Sentenac 2003). Several recent studies have focused the plant adaptation mechanisms to low K^+ under elevated salts or salinity-free conditions. Hence, these mechanisms must be explored to better understand salinity tolerance in crop plants. The studies focusing on these mechanisms have concluded that sufficient or higher K^+ availability imparts salinity tolerance to crop plants, while low K^+ availability in soils makes salinity stress highly devastating for crop plants.

The Na^+-induced K^+ exclusion form root and leaf cells is the most obvious effect of salinity stress on K^+ homeostasis (Wang et al. 2009; Demidchik et al. 2014). The K^+ exclusion has been concluded to be the exclusive result of Na^+ entering into the cytoplasm. The Na^+ inclusion depolarizes membrane potential below the resting potential. This depolarization consequently activates K^+ outward rectifier channels, such as GORK (guard cell outward rectifying K^+ channel), through which K^+ is excluded from the plant cells and tissues. Thus, maintenance of higher inside negative potential through prevention of membrane depolarization for enhancing intracellular K^+ retention (inhibition of K^+ efflux) (Falhof et al. 2016) would be a salinity tolerance mechanism of crop plants. Recent studies have identified that retention capacity of intracellular K^+ is a crucial mechanism for salinity stress tolerance (Janicka-Russak and Kabała 2015). The PM H^+-ATPases and tonoplast H^+-ATPases/H^+-PPases, K^+ transporters, NHX antiporter, and SOS1 proteins have been considered as vital players in the process of subsiding salinity stress and negative effects of low K^+ availability on crop plants (Pottosin and Dobrovinskaya 2014; Janicka-Russak and Kabała 2015; Falhof et al. 2016). It is concluded that K^+ efflux and influx mechanism are really crucial for salinity tolerance in crop plants. Thus, equipping crops with these mechanism will assure survival and sustained production under elevated salt levels in the soil.

17.7 Vacuolar Compartmentation and Ion Homeostasis

The ability of different plant species to tolerate elevated salinity levels is determined by the Cl^- partitioning between different types of roots and shoots cells. Some evidence report that Cl^- is accrued in the epidermis cells of leaves, which reduces the Cl^- toxicity photosynthetically important mesophyll cells. The differential ability to exclude Cl^- from mesophyll cells has been observed in two barley cultivars where salt-tolerant genotype was better able to exclude Cl^- than salt-sensitive genotype (Huang and Van Steveninck 1989). A more sophisticated analyses conducted by using single-cell-sampling techniques revealed that Cl^- accumulation increased in both epidermal and mesophyll cells with rising NaCl (Fricke et al. 1996). It was also concluded that photosynthesis in salt-stressed plants was mildly affected, which gives rise to the doubts that Cl^- accumulation in epidermal cells is linked with salinity tolerance. Fricke et al. (1996) also revealed that the Cl^- accumulation in epidermal cells was three times higher than the Cl^- accumulation in mesophyll cells. However, regardless of this fact, Na^+ and K^+ accumulation was similar in both types of cells. James et al. (2006) studied the accumulation of Cl^- in two barley cultivars differing in a salinity tolerance. It was concluded that Cl^- preferred epidermis cells over mesophyll cells for accumulation. Similar pattern of Cl^- accumulation was observed in both sensitive and tolerant cultivar, which indicates that Cl^- accumulation in a specific type of cells could not be concluded a major trait conferring salinity tolerance in crop plants.

The Cl^- accumulation in salt glands or bladders is one other form of intercellular compartmentation. Halophyte group of crop plants possesses these special structures, which can store Cl^- (and even Na^+), helping plants to withstand the negative effects of elevated salt levels. The secretion of Cl^- through salt glands can be concluded as an important salinity tolerance trait as >20% Cl^- in the leaves of *Leptochloa fusca* under 100 mm NaCl level was secreted by salt glands (Jeschke et al. 1995). Different studies have focused the salt glands possessed by some halophytic species, i.e., *Bienertia sinuspersici* and *Limonium sinense* (Ding et al. 2009; Park et al. 2009). A cation-chloride cotransporter (CCC) was localized to leaf trichomes and hydathodes in *Arabidopsis* (Colmenero-Flores et al. 2007). The ultimate role of CCC is still unclear, however, investigating whether CCC are also present in the slat glands of halophyte species to infer the possible Cl^- efflux (and Na^+) from leaves.

The salinity tolerance of the crop plants could not always be attributed to the low concentrations of Cl^- and Na^+ in the shoots. The Cl^- tolerance largely varies among genotypes of a same species. Therefore, salinity tolerance could not be attributed to the shoot Cl^- concentration. The Cl^- and Na^+ are excluded by most of the plant species up to a certain level (90–98%; Munns 2005); however, effective Cl^- and Na^+ sequestration in the vacuole to prevent them to accumulate at toxic levels will impart ultimate salinity tolerances to crop plants. Even the halophyte plant species are unable to elevate levels of cytoplasmic Cl^-; thus they have evolved strategies which effectively sequester Cl^- into vacuoles to control the accumulation of Cl^- and other ions through turgor-driven growth (Flowers et al. 1977; Glenn et al. 1999).

The direct measurements of Cl^- fluxes and its concentration in the vacuoles of the plants intact from salinity through experimental studies are difficult; however, there exist some estimates conducted through X-ray microanalysis, intracellular ion-sensitive microelectrodes, tracer compartmental analysis, or Cl^--sensitive fluorescent probes (Hajibagheri and Flowers 1989; Felle 1994; Britto et al. 2004; Lorenzen et al. 2004). All these estimates have concluded that the vacuole of plant cells are able to accumulate Cl^- up to 500 mm (Cram 1973).

There have been some indirect confirmation that efficient Cl^- sequestration in the vacuole imparts salinity tolerance to some plant species. The salinity-tolerant genotypes of citrus, grapevine, and *Lotus* had low Cl^- in shoots, while accumulated more Cl^- in the roots compared to their respective sensitive genotypes (Storey and Walker 1998; Storey et al. 2003). These findings suggest that the tolerant genotypes efficiently compartmentalized the Cl^- in root vacuoles. Some avocado rootstocks have been found to possess high amount of Cl^- in the leaves, which has been linked to their salinity tolerance (Xu et al. 2000). Similarly, some lupin cultivars also accumulated more Cl^- in the leaves for salinity tolerance (Van Steveninck et al. 1982).

Some direct comparison among different genotypes has concluded that effective compartmentation of intracellular Cl^- imparts salinity tolerance to crop plants. Hajibagheri et al. (1989) compared two maize genotypes differing salinity tolerance for cytoplasmic Cl^- concentrations. It was concluded that sensitive genotypes accumulated more root cytoplasmic Cl^- concentrations than tolerant genotype. The accumulated amount of Cl^- was comparable to accumulated amount of Cl^- (350 mm for barley at 100 mm NaCl) in barley genotypes (Britto et al. 2004). Flowers and Hajibagheri (2001) compared two barley genotypes having differential ability of salt tolerance through X-ray microanalysis. It was concluded that cytoplasmic and vacuolar concentrations of Cl^- (and Na^+) were similar; however, the tolerant barley cultivar accumulated half of the Cl^- concentration accumulated by the sensitive genotype. The higher concentration of ions in the cell wall of sensitive genotype reduced turgor, which ultimately resulted poor growth. To assess whether vacuolar Cl^- sequestration is involved in salinity tolerance, further studies are needed focusing on the comparison of genotypes having differential salt tolerance level, but having similar leaf or root Cl^- concentrations.

17.8 Ion Sensing and Gene Defense Activation

Several genes imparting salinity tolerance to crop plants have been identified through the use of genetic damage or gain of function methods (Zhu 2002, 2003; Apse and Blumwald 2007; Pardo and Rubio 2011; Peleg et al. 2011). The identified genes encode transport determinants mediating Na^+ homeostasis (Plett and Møller 2010; Pardo and Rubio 2011; Peleg et al. 2011). These identified determinants mainly from glycophyte plant species enhance the salinity tolerance capabilities of halophytic species as well as crop plants (Oh et al. 2010, 2012; Dassanayake et al. 2011a, b; Munns et al. 2012). There has been a lot of conversation on the underlying mechanisms and determinants imparting salinity tolerance to halophytes and glycophytes. There are emerging evidence which provide a degree of systematic clarification that why halophytes are better able to tolerate elevated salt levels (Amtmann 2009; Dassanayake et al. 2011b; Oh et al. 2012).

The halophytic plant species possess “superior” alleles and novel loci involved in Na^+ homeostasis and salinity tolerance (Edelist et al. 2009; Dassanayake et al. 2011a, b; Oh et al. 2012). There have been several critical questions relating to Na^+ homeostasis in halophytic plant species. These critical questions include the following: Do halophytes have unique transport determinants? Do halophytes have orthologous determinants with diverse actions? And do halophytes differentially control transport protein action or expression of encoding genes to increase salinity tolerance (Oh et al. 2009, 2012; Plett and Møller 2010; Dassanayake et al. 2011b)? The rapidly advancing omics technologies such as massively parallel sequencing, whole genome sequencing, and sequencing by genotyping as well as phenotyping could facilitate to find the answers of all these critical questions providing valuable insights on the salinity tolerance mechanisms of halophytic plant species (Lin et al. 2004; Takeda and Matsuoka 2008; Dassanayake et al. 2011b; Oh et al. 2012).

The well-known and suggested salinity tolerance signaling pathway includes facilitation of ionic and osmotic homeostasis, growth regulation, and regulation of development (Zhu 2002). The SOS proteins, phospholipid, ROS, ABA, cytokinin, Ca^{2+}, hyperosmotic and osmotic solute, and kinase/phosphatase pathways are the probable pathways integrated to cope salinity tolerance/acclimation in plant species, which are mainly concluded from the studies conducted on *Arabidopsis* (Gong et al. 2001; Zhu 2002; Qin et al. 2011; Reddy et al. 2011; Suzuki et al. 2012). It has been described that several determinants are governed and regulated by abovementioned networks and various transcriptomic and proteomic analyses have identified that these determinants play a crucial role in salinity tolerance of crop plants (Zhu 2002; Golldack et al. 2011; Pérez-Alfocea et al. 2011; Singh et al. 2011; Zhang et al. 2012).

The Na^+ homeostasis, as described above, is mediated by a highly defined SOS Ca^{2+} signaling pathway (Zhu 2002, 2003). The Na^+ signal perception is unclear; however, Ca^{2+} is known to be a secondary messenger in signal transduction (Zhu 2002, 2003; Conde et al. 2011). The activates of SOS1 Na^+/H^+ antiporter are regulated by SOS pathway, which facilitates Na^+ efflux across the plasma membrane (Zhu 2002, 2003; Pardo and Rubio 2011). Calcineurin B and neuronal Ca^{2+} sensor-like protein SOS3 decode the NaCl-induced cytosolic Ca^{2+} increase (CBL4). The CBL4 is a myristoylated protein with EF-hand Ca^{2+}-binding places (Zhu 2002, 2003; Gong et al. 2004; Sánchez-Barrena et al. 2005; Tracy et al. 2008; Pardo and Rubio 2011). Ca^{2+}-activated SOS3 interacts with the auto-inhibitory domain of SOS2 (*CIPK24*), a member of the SnRK family (Zhu 2002, 2003; Gong et al. 2004; Cosello et al. 2011; Kulik et al. 2011; Pardo and Rubio 2011). SOS3 binding to the SOS2 auto-inhibitory domain triggers kinase action and enables localization of the SOS2-SOS3 complex (Zhu 2002, 2003; Sánchez-Barrena et al. 2007; Pardo and Rubio 2011). SOS2 then acquaintances with SOS1 Na^+/H^+ in the plasma membrane, phosphorylating the transporter and triggering Na^+ exclusion (Zhu 2002, 2003; Martínez-Atienza et al. 2007; Pardo and Rubio 2011; Quintero et al. 2011). Several genes and gene networks are being identified with each passing day with technological advancements. Thus a comprehensive understanding of nutrient homeostasis requires sound knowledge of different mechanisms involved. Although, several mechanisms are discussed in this chapter, still gaps exist which need to be filled through comprehensive studies on salt tolerance and nutrient homeostasis in plants. Moreover, the studies focusing on mediating nutrient homeostasis could provide valuable insights on inducing salinity tolerance in plant species through the manipulation of nutrient homeostasis.

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Chapter 18

Ion Homeostasis and Antioxidant Defense Toward Salt Tolerance in Plants

Pedro García-Caparrós, Mirza Hasanuzzaman, and María Teresa Lao

Abstract The increase of salinity in the soil represents a great threat at worldwide level since it reduces the plant growth and the productivity. The main problems of salinity are related to the osmotic effect and specific ions. The changes in cytosolic Ca^{2+} concentration are supplied from the apoplast or internal stores like mitochondria or vacuoles, and they educe several purposes at cellular levels such as signal transduction in plant-defense responses against stresses. Even though the Cl^- movement response to salt stress is less investigated, it is well known that their entrance through plasma membrane is related with a raising external Cl^- concentration and the relocation of Cl^- from the cytoplasm into the vacuole of root cells ends with delimitated concentrations. Due to the chemical uniformity between Na^+ and K^+, there is a high competence between them for binding sites in different physiological processes such as enzymatic reactions, protein synthesis, and ribosome functions; therefore, the cellular maintenance of Na^+/K^+ homeostasis is essential to overcome the salinity in plants. All of these responses are triggered by plants to maintain the ion homeostasis because it is an essential process for growth during salt stress. Also, plant cells are responsible for the reduction of toxic ions and the accumulation of crucial ions to maintain the ion homeostasis. Antioxidant defense system of plants is regarded as one of the vital mechanisms of salt stress tolerance by which plants cope with oxidative stress. Several recent studies indicated that both ion homeostasis and antioxidant defense systems are closely associated with salt tolerance. This review will be focused on current progress of nutrient homeostasis and antioxidant defense in plants under increasing saline conditions.

Keywords Antioxidant defense · Ion homeostasis · Reactive oxygen species · Salinity

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18.1 Introduction

Salinity is an abiotic stress that originates fields unproductive reducing the plant growth and yield. It is estimated that 830–950 million hectares in the world is altered (Teakle and Tyerman 2010; García-Caparrós et al. 2017).

The effects of this abiotic stress in plants can be classified in two main ways: an osmotic effect related to the difficulties in the water uptake by roots due to the high concentrations of salts in the medium and an ionic effect related to the repression of many physiological and biochemical processes by the presence of toxic ions (Munns and Tester 2008). Excess creation of reactive oxygen species (ROS) and thus oxidative stress is one of the early responses and signaling episodes in plants under salinity conditions (Hasanuzzaman et al. 2013). Homeostasis is the trend of a cell or organism to avoid perturbations in their key biochemical and physiological processes as a response to adverse environmental conditions; therefore nutrient homeostasis in a plant is essential for its growth and is depending on the ion fluxes (Nieves-Cordones et al. 2012).

It is well known that under non-saline conditions, cells have to keep high concentrations of K^+ and low concentrations of Na^+, but under saline conditions this trend is the converse. Both ions are crucial in several physiological processes such as the activation of enzymes and the preservation of membrane potential and osmotic potential of the cell for cell volume adjustment and cell function (Hajiboland 2012).

To avoid these harmful effects, plants have triggered different biochemical and physiological mechanisms in order to reduce the concentration of toxic ions. These mechanisms include the ion homeostasis through the performance of different transporters and the accumulation of antioxidative enzymes (García-Caparrós et al. 2016). Approaches in enhancing antioxidant defense in plants have been conceding as one of the vital tasks for plant biologists to produce salt-tolerant crop varieties. The main subject of this chapter will be the ion homeostasis and the antioxidant defense system in plants under saline conditions.

18.2 Calcium Homeostasis

Calcium is considered as a crucial plant nutrient since it is involved in the maintenance of membrane integrity in cell walls and membranes and the control of plant development (Bose et al. 2011). Nevertheless, this element can be destructive at high concentrations due to its capacity to ligand binding with proteins, membranes, and organic acids which generates combination of proteins and nucleic acids and precipitation of phosphates resulting in changes of lipid membrane composition (Case et al. 2007).

Calcium is incorporated from the soil medium through the roots and translocated via xylem to the stem. The movement of this ion in the xylem is high, but the uptake of Ca^{2+} is restricted in apical roots where Casparian band is not present or disorganized due to the unsuberization of endodermal cells (White and Broadley 2003).

18.2.1 Calcium Transporters

The transporters of Ca^{2+} (Table 18.1) in higher plants can be categorized as:

18.2.2 Ca^{2+}-ATPases

Ca^{2+}-ATPases are included on the superfamily of P-type ATPases and they require energy supplied by ATP. These transporters operate with submicromolar concentrations of Ca^{2+} and can be classified in two groups: P2A-ATPase [or ER-type Ca^{2+}-ATPase (ECA)] and P2B-ATPase [or autoinhibited Ca^{2+}-ATPase (ACA)]. The former can be located in the plasmatic membrane besides in endomembranes, while the latter is exclusively found in endomembranes (Møller et al. 2010). The process of ATP hydrolysis occurs if Ca^{2+} has been tied up in the membranous region of the Ca^{2+}-ATPase. As a consequence, under salt stress, the presence of Na^+ reduces the

Table 18.1 Calcium transporters under saline conditions

Species	Name	Salinity dose and duration	Function	References
Glycine soja	GsACA1, P-type IIB Ca^{2+}-ATPase	200 mM NaCl, 3 weeks	Influx of Ca^{2+} into the cytosol	Sun et al. (2016)
Oryza sativa	OsACA6, P-type IIB Ca^{2+}-ATPase	200 mM NaCl, 3 weeks	Influx of Ca^{2+} into the cytosol	Huda et al. (2013)
Arabidopsis thaliana	AtNCL, (CAXs)	150 mM NaCl, 1 week	Maintenance of Ca^{2+} homeostasis	Wang et al. (2012)
Oryza sativa	OsCAX4	150 mM NaCl, 1 week	Vacuolar Ca^{2+} transporter	Yamada et al. (2014)
Glycine soja	GsCBRLK, calcium/calmodulin	200 mM NaCl, 3 weeks	Protein phosphorylation	Yang et al. (2010)
Oryza sativa	OsMSR2, calcium/calmodulin	150 mM NaCl, 3 weeks	Salt tolerance through ABA-mediated pathways	Xu et al. (2011)
Arabidopsis thaliana	Calcineurin B-like 10	200 mM NaCl, 1 week	Regulate salt export across the plasma membrane	Kim et al. (2007)
Arabidopsis thaliana	Calcineurin B-like 10	40 mM NaCl, 3 weeks	Independence from SOS pathway	Monihan et al. (2016)

binding of Ca^{2+} to the plasma membrane resulting in an efflux of Ca^{2+} reducing the inner supplies from endomembranes (Morth et al. 2011).

18.2.3 Ca^{2+}-Exchangers (CAXs)

Cation proton/exchangers (CAXs) are another kind of energy ion transporters controlled by a proton (H^+) gradient with diverse physiological roles such as the inclusion of Ca^{2+} in the vacuole from the cytosol of a cell (Pittman and Hirschi 2016). The homeostasis of Ca^{2+} in *Arabidopsis* is controlled by six genes (AtCAX1 to AtCAX6) (Manohar et al. 2011). CAX1 may be controlled via an N-terminal autoinhibitory domain, which is bound to an adjacent region within the N-terminus (Mei et al. 2007). Also, there are other processes of adjustment like the generation of CAX complex through combination between CAX1 and CAX3 (Zhao et al. 2009), phosphorylation (Pittman et al. 2002), and the adjustment of pH (Zhao et al. 2008). This regulation of pH levels plays a crucial role in the activation of defense response mechanisms under salt stress conditions (Kader and Lindberg 2010).

18.2.4 Calmodulin

Calmodulin (CaM) is a prototypical Ca^{2+}-sensor protein formed by a couple of Ca^{2+}-binding sites named EF hands responsible for the control of different biological processes. Calmodulin is located in different organelles like the apoplast, nucleus, and endoplasmic reticulum (Zheng et al. 2015). It is well documented that CaM can change its conformational form from globular structure to an open conformation allowing the combination with proteins mainly due to the effect of Ca^{2+} binding (Yamniuk and Vogel 2005). CaM is considered as a main controller in the resistance to salt and osmotic effects since it simulates the activity of glyoxalase I, an enzyme well related to the capacity of resilience to salinity conditions in plants (Kaur et al. 2014).

18.2.5 Calcineurin B-Like Proteins

Calcineurin B-like sensors known as CBLs are proteins of small size formed by two globular domains joined by a short linker. Each domain is composed of two EF-hand motifs as Ca^{2+}-binding domain, and they affect only a family of Ser/Thr protein kinases (Zhang et al. 2014). These proteins may function as positive regulators of salt responses as reported by Li et al. (2013) in *Arabidopsis thaliana*.

18.2.6 Calcium Influx and Efflux

The cytosolic Ca^{2+} increases under increasing saline concentrations and the maintenance of an adequate cytosolic Ca^{2+} concentration are essential to preserve the ion homeostasis in the plant. The Ca^{2+} influx is controlled by two permeable channels: depolarization-activated (DACCs) and hyperpolarization-activated (HACCs). Considering their qualities in the process of activation, Ca^{2+} channels can modify the variables of Ca^{2+} influx and the resulting Ca^{2+} signature (Demidchik and Maathuis 2007). As a result, plants are able to render variable signs into different Ca^{2+} signatures (Miedema et al. 2008).

The main aims of Ca^{2+} efflux mechanisms are the preservation of Ca^{2+} concentration in the cytosol and the replenishment of Ca^{2+} stores after Ca^{2+} concentration in the cytosol signaling is completed. The process of Ca^{2+} efflux is controlled by Ca^{2+}-ATPases and Ca^{2+}-exchangers (CAXs). It is well known that CAXs are responsible for the decrease of Ca^{2+} concentration after signalization while Ca^{2+}-ATPases are necessary to conserve the low concentration of Ca^{2+} (Bose et al. 2011).

18.3 Chloride Homeostasis

Chloride is an essential micronutrient responsible for different roles like synchronization of enzymatic activities in the cytoplasm, cofactor in photosynthesis, involvement in pH regulation, and regulation of membrane potential and turgor through the counteraction of anions (Teakle and Tyerman 2010). Also, it is a plant micronutrient with regulatory roles in transpiration, nutrition, and growth (Li et al. 2017).

Plants uptake chloride from soil solution to the Cl^- anion through an energetic process. Previous studies have reported that the movement of Cl^- transport through the cell membrane can be performed in two ways: the former requires a $2H^+/Cl^-$ symporter and the latter takes place via antiport using hydroxyl ions activated by ATP. The activation of ATP depends on the pH gradient generation by Cl^-; this is due to dissipation by the anions of the membrane potential produced by transmembrane transport of protons (White and Broadley 2001).

18.3.1 Chloride Transporters

The transport of chloride in higher plants can be performed through different transporters (Table 18.2).

Table 18.2 Chloride transporters under saline conditions

Species	Name	Salinity dose and duration	Function	References
Arabidopsis thaliana	AtCLCc	50 mM NaCl, 3 weeks	Regulation of stomatal movements	Jossier et al. (2010)
Arabidopsis thaliana	AtCLCg	75 mM NaCl, 3 weeks	Cl^- homeostasis	Nguyen et al. (2016)
Glycine max	GmCLC1	150 mM NaCl, 6 days	Regulation of Cl^- transport	Wei et al. (2016)
Glycine max	GmCLC1	125 mM NaCl, 1 week	Regulation of Cl^- transport	Li et al. (2006)
Vitis vinifera	VviCCC	100 mM NaCl, 6 weeks	Salt exclusion of Cl^- from the root xylem	Henderson et al. (2015)

18.3.2 Chloride Channel (CLC) Proteins

CLCs are responsible for the regulation of vacuolar sequestration of Cl^- and NO_3^-, which makes them possible roles in the regulation of Cl^- homeostasis. In *Arabidopsis*, researchers have reported six homologues known as AtClC-A to AtClC-F. AtClC-A is responsible for outwardly rectifying and strongly NO_3^--selective currents. In this homologue, there are two glutamate residues known as "gating" and "proton." It is important to highlight that the proton residue confers to itself the possibility to work as a NO_3^-/H^+ antiporter. The high synchronicity between AtClC-A and AtClC-B (87% similarity) and the maintenance of critical residues result in homologues with the same capacities (Zifarelli and Pusch 2010).

AtClC-C is another homologue placed in the tonoplast and responsible for the movement of Cl^- through the tonoplast as reported by Jossier et al. (2010).

AtClC-D together with H^+-V-ATPase is responsible for the maintenance of a correct level of acidification in the trans-Golgi network (TGN) through the flux of counteranions like Cl^- and NO_3^- (Von der Fecht Bartenbach 2007).

AtClC-E and AtClC-F are more related to prokaryotic chloride channels than the other homologues in *Arabidopsis*. These homologues are placed in thylakoids and cis-Golgi vesicles (Marmagne et al. 2007).

18.3.3 Electroneutral Cation-Chloride Cotransporters (CCCs)

CCCs are uncharged transporters mediating responsible for the delivery of Cl^- connected with K^+ and/or Na^+ across the plasma membrane (Colmenero-Flores et al. 2007). CCCs can be divided into three members: the first members named as KCC (K^+:Cl^- cotransporters), the second members named as NCC (Na^+:Cl^- cotransporters), and the last member named as NKCC (Na^+:K^+:Cl^- cotransporters). Different studies in ion transport have reported that all the members have a high demand of both Cl^- and at least one cation (Na^+ and/or K^+) (Colmenero-Flores et al. 2007; Köhler and Raschke 2000) suggesting that CCCs could be a feasible aspirant gene for xylem retrieval of Cl^- under saline conditions.

18.3.4 Chloride Influx and Efflux

Under saline conditions, it is essential to control the influx and efflux of chloride in plants. Chloride influx is an active process mediated by high-and low-affinity Cl^-/H^+ symport transporters. The process of Cl^- efflux is passive where the movement of anions from the cytoplasm to the external medium is through anion efflux channels (Brumos et al. 2010). As a consequence, the building up of Cl^- will be related to the unidirectional active influx and passive efflux (Teakle and Tyerman 2010).

18.4 Potassium Homeostasis

Potassium is a mineral nutrient well demanded by plants and participates in essential biological processes such as enzyme activation, membrane transport, anion neutralization, and osmoregulation (Wang and Wu 2013). The soil solution has a concentration of K^+ ranging from 0.025 to 5 mM (Maathuis 2009), but the needs of the plants are higher representing between 2% and 10% of K per dry weight (50–250 mM), and as a consequence plants are effective on the management of a continuous cytosolic K^+ concentration that varies between 100 and 200 mM (Britto and Kronzucker 2008).

The process of K^+ uptake in plants can be performed through two different transporters: high-affinity that function with low external potassium concentration (below 0.2 mM) and low-affinity that function with high external potassium concentration (above 0.3 mM) (Nieves-Cordones et al. 2014).

18.4.1 Potassium Transporters

Potassium transporters (Table 18.3) are discerned in two major groups. The former group is comprised of (1) KUP/HAK/KT transporters, (2) HKT transporters, and (3) K^+/H^+ antiporters. The latter group is composed of three members of permeable channels: (1) Shaker-type potassium channels, (2) “two-pore” potassium channels, and (3) nonselective cation channels (NSCCs) (Benito et al. 2014).

Table 18.3 Potassium transporters under saline conditions

Species	Name	Salinity dose and duration	Function	References
Thellungiella salsuginea	TsAKT1	300 mM NaCl, 2 weeks	Higher K^+ specificity	Ali et al. (2012)
Kandelia obovata	AKT1	400 mM NaCl, 15 days	Increase of K^+ uptake	Chen et al. (2013)
Suaeda salsa	SsAKT1	150 mM NaCl, 1 day	Maintenance of K^+ nutrition through low-affinity system	Duan et al. (2015)
Populus euphratica	PeTPK1	150 mM NaCl, 3 weeks	Maintenance of K^+ homeostasis	Wang et al. (2013)
Arabidopsis thaliana	HAK5	30 mM NaCl, 18 days	Improvement of K^+ acquisition	Nieves-Cordones et al. (2010)
Hordeum vulgare	HvHKT2;1	100 mM NaCl, 2 weeks	Higher Na^+ uptake and translocation to leaves	Mian et al. (2011)
Oryza sativa	OsHKT2;2/1	100 mM NaCl, 18 days	Improvement of root K^+ uptake	Oomen et al. (2012)
Solanum lycopersicum	LeNHX2	120 mM NaCl, 40 days	Improvement of K^+ homeostasis	Huertas et al. (2013)
Hordeum vulgare	HvNHX4	150 mM NaCl, 4 days	Improvement of K^+ homeostasis	Ershov et al. (2007)
Arabidopsis thaliana	AtCHX21	100 mM NaCl, 4 weeks	Regulation of xylem Na^+ concentration	Hall et al. (2006)

18.4.1.1 KUP/HAK/KT Transporters

KUP/HAK/KT transporters are placed in different organelles like the plasma membrane and the tonoplast, and they are responsible for high- and low-affinity K^+ uptake processes. This group of transporters is analogous to other K^+ transporters like the transporter KUP in bacteria and the transporter HAK1 in fungus. These transporters are essential in nutrient acquisition and the management of the development (Wang and Wu 2013).

18.4.1.2 HKT Transporters

HKT proteins are considered essential in the process of Na^+ uptake and recirculation in plants subjected to saline conditions; thus they are important components of salinity tolerance in plants. These transporters can be classified in two categories according to their transport selectivity. The former category is known as Na^+ uniporters, whereas the latter category can be Na-K symporters and also Na^+ uniporters at high Na^+ levels (Waters et al. 2013).

18.4.1.3 K^+/H^+ Antiporters

These transporters belong to the family of cation/proton exchanger (CHX) (CPA2 family) composed of 28 members. In the *Arabidopsis* genome, there are six K^+ efflux antiporters from KEA1 to KEA6. Besides these transporters, in *Arabidopsis* there are other families such as CPA1 (monovalent cation: proton antiporter with eight members) and NhaD with two members (Wang and Wu 2013).

18.4.2 Potassium-Permeable Channels

18.4.2.1 Shaker-Type Potassium Channels

These channels are responsible for K^+-selective voltage-gated currents under hyperpolarized and depolarized potential conditions in the plasma membrane (Gambale and Uozumi 2010). They are classified in three groups according to their voltage reliance. The first group known as inward-rectifying channels (AKT1, KAT1, KAT2, and SPIK) is characterized by their activation through the hyperpolarization potential, and they participate in the process of K^+ uptake. The second group known as outward-rectifying channels (SKOR and GORK) is identified by their activation through depolarization potential, and they are involved in the process of K^+ efflux. The latter group known as weakly rectifying channels (AKT2/3) is denoted by their activation by hyperpolarization potential, and they play essential roles in the processes of K^+ uptake and K^+ release based on the membrane potentials (Wang and Wu 2013).

18.4.2.2 "Two-Pore" Potassium Channels

These potassium channels show a high Ca^{2+} reliance and outward rectification and they are placed in the tonoplast. In the *Arabidopsis* genome, it is possible to find two groups of these channels like KCO-1P with one member and KCO2-P with five members (Shabala and Pottosin 2010). The understanding of how these channels participate in the salinity tolerance in plants is scarce. Nevertheless, Shabala and Pottosin (2014) reported the presence of one of these channels known as TPK5 (KCO5) in the vacuole that participates in the maintenance of cytoplasmic K^+ concentrations and/or the exchange of K^+ for Na^+.

18.4.2.3 Nonselective Cation Channels

The latter group of potassium-permeable channels is known as nonselective cation channels (NSCCs), and they are placed in different sites like the plasmatic membrane and tonoplast. These channels have a higher preference for cations than anions and they possess K^+/Na^+ selectivity ratios which range from 0.3 to 3. There are different reasons by which NSCCs can be blocked: depolarization and hyperpolarization initiation, weakly voltage, calcium initiation, and mechanosensitive, cyclic nucleotide-gated and glutamate-gated channels (Pottosin and Dobrovinskaya 2014).

18.4.3 Potassium Influx and Efflux

Under saline conditions, it is crucial to maintaining an adequate K^+ flux in higher plants. The directional movement of K^+ is controlled by the equilibrium potential (EK) and the membrane potential (Em) in cells. Considering the aforementioned, if the value of Em is more negative than EK, there is an influx of K^+ through the channels, but if occurs the contrary (Em less negative than EK), then occurs an efflux from the inside of the cells. As a consequence, the process of K^+ uptake requires that root cells present a value more negative of Em to ensure K^+ influx and avoid K^+ efflux under deficiencies of K^+ (Sun et al. 2009).

18.5 Sodium Homeostasis

Sodium is a functional nutrient in plants involved in different metabolic functions due to the parallelism between sodium and potassium. These functions include being a cofactor in enzyme activation, the stabilization of the active conformation of enzymes and possible membranes, cytoplasmic volume regulation, energy conservation across membranes, and the regulation of cytoplasmic pH (Pessarakli 2014). Nevertheless, an increase of sodium concentration can result in a destabilization of membranes and proteins affecting negatively fundamental processes like the division and expansion in a cell, primary and secondary metabolism, and the homeostasis of mineral nutrients (Hasegawa 2013).

It is well known that Na^+ relocation from the root zone to the other organs of the plants takes place by flow mass controlled mainly by the pressure gradient (Taiz and Zeiger 2010). Thereupon, the movement of Na^+ from the root zone to the xylem takes place via symplastic, apoplastic, or intercellular spaces until to the endodermis with the Casparian strip which limits the apoplastic movement (Plett and Møller 2010).

18.5.1 Sodium Transporters

The main transporters of sodium (Table 18.4) in higher plants can be classified as:

18.5.1.1 HKT Transporters

The HKT (high-affinity potassium transporter) family is classified in two distinct groups in compliance with their delivery features. The principal distinctive characteristic of these transporters is the conformational order of amino acids of the first pore domain (PD) (Platten et al. 2006). For instance, the conformational order (S-G-G-G) including a serine is representative of the members of the group I (HKT1), whereas in members of group II (HKT2), serine is replaced by guanine showing this order (G-G-G-G) (Maser et al. 2002). The presence of S or G in the pore domain

Table 18.4 Sodium transporters under saline conditions

Species	Name	Salinity dose and duration	Function	References
Oryza sativa	OsHKT1;1	100 mM NaCl, 1 week	Reduction of Na^+ accumulation in shoots	Wang et al. (2015)
Oryza sativa	OsHKT1;4	100 mM NaCl, 3 weeks	Na^+ exclusion from leaf blades	Suzuki et al. (2016)
Sorghum bicolor	SbHKT1;4	200 mM NaCl, 2 weeks	Maintenance of Na^+/K^+ balance	Wang et al. (2014)
Hordeum vulgare	HvHKT2;1	100 mM NaCl, 4 weeks	Translocation of Na^+ to the shoot	Mian et al. (2011)
Thellungiella salsuginea	TsHKT1;2	300 mM NaCl, 2 weeks	Higher specificity by K^+ instead of Na^+	Ali et al. (2012)
Zygophyllum xanthoxylum	ZxNHX	50 mM NaCl, 4 weeks	Maintenance of Na^+/K^+ homeostasis	Yuan et al. (2015)
Helianthus tuberosus	HtNHX1; HtNHX2	300 mM NaCl, 24 h	Mediation of $Na^+(K^+)/H^+$ exchange	Zeng et al. (2017)
Mesembryanthemum crystallinum	McNHX2	500 mM NaCl, 1 week	Na^+ homeostasis	Villicaña et al. (2016)
Triticum aestivum	TaSOS1, 2, 3	200 mM NaCl, 8 weeks	Active efflux of toxic Na^+ from the cytosol	Sathee et al. (2015)
Populus daviana × *Populus bolleana*	PtSOS2	300 mM NaCl, 3 weeks	Na^+ extrusion	Yang et al. (2015)

results in changes in the cation specificity of the transporter. As a consequence, the members of the group I show a Na^+ uniport, whereas the members of the group II are characterized by Na^+/K^+ symport (Kronzucker and Britto 2011).

18.5.1.2 NHX Transporters

Plant NHX proteins are included in a superfamily of monovalent cation/proton antiporters (CPAs). This superfamily is comprised of two categories: CPA1 and CPA2, respectively. In the first category are included plant NHX proteins being present in unicellular and multicellular organisms. In the second category are included cation/H^+ exchangers (CHXs) and K^+ efflux antiporters (KEA) (Bassil et al. 2012). The first of them is responsible for the Na movement into the vacuole according to the electrochemical gradient of protons promoted by the V-ATPase and V-PPase enzymes (Bassil and Blumwald 2014).

18.5.1.3 SOS Transporters

SOS transporters are crucial in the control of ion homeostasis in cells because they are involved in the process of Na^+ exclusion. The modulation of the transcription of SOS1 under high saline conditions is achieved by SOS2 and SOS3. Moreover, this transporter together with a protein kinase (CIPK24/SOS2) and a calcium sensor (CBL4/SOS3) is the main responsible for the control of ion homeostasis at cellular level (Ji et al. 2013).

18.5.2 Sodium Influx and Efflux

It is well known that sodium uptake, transport, and compartmentation are essential for plants for them to remain alive under salinity. The influx of Na^+ in only one direction is depending on different groups of transporters. One of them is transporters of high-affinity K^+ ((HKT) types 1 and 2 and HAK/KUP/KT and AKT1). Others are transporters of low-affinity K^+ like cation-Cl^- cotransporter, and besides nonselective cation channel (NSCC) members are involved in the process of influx of Na^+ (Kronzucker and Britto 2011).

In addition, it is necessary to point out that the process of Na^+ influx is controlled by Ca^{2+}-sensitive and Ca^{2+}-insensitive processes. Ca^{2+}-sensitive Na^+ influx is influenced by nonselective cation channels (NSCCs). Nevertheless, this sensitive process requires the involvement of Ca^{2+}-insensitive influx of Na^+ through HKT transporters in order to accomplish the process of Na^+ influx (Plett and Moller 2010).

As far as efflux of Na^+ is concerned, Maathuis et al. (2014) reported that is an active process with energy consumption. This efflux occurs across the plasma membrane, and the transporter involved is SOS1, which operates with a secondary active transport activated by the H^+ gradient across the plasma membrane (Hasegawa 2013).

18.6 K^+ and Na^+ Homeostasis Under Saline Conditions

It is generally accepted that under saline conditions, the maintenance of an adequate ion concentration inside the cell is essential to the metabolism of plant cells. To achieve this homeostasis, plant cells are responsible for the reduction and accumulation of ion concentrations in adequate levels to regulate the ion flux. It is well known that K^+ and Na^+ compete for the same binding sites so if there is a depolarization in the membrane by an increase of Na^+ concentration, the main consequence will be a decrease of K^+ uptake and an increase of K^+ efflux through outward-rectifying channels (Adams and Shin 2014).

The maintenance of high K^+ levels and low Na^+ in the cytosol of a cell is controlled by H^+-ATPase (active transport) and channels and cotransporters (secondary transport). One way to reduce the concentration of Na^+ in a cell is the exclusion and its compartmentation in the vacuole; therefore this mechanism has a high significance in the salt tolerance at cellular level (Deinlein et al. 2014).

18.7 ROS Metabolism and Antioxidant Defense System Under Salinity

Unlike other abiotic stresses, salt stress also incurs oxidative stress due to excess generation of ROS. Plants have well-developed antioxidant system composed of nonenzymatic and enzymatic antioxidants. But under stressful condition, ROS production goes beyond the capacity of the antioxidant defense system and as a consequence oxidative stress occurs. Different metabolic pathways are interlinked with ROS metabolism in plants under salt stress. Moreover, ROS sensory and signaling networks as well as the cross talk with other signaling pathways become an important consideration in understanding for salt tolerance (Hossain and Dietz 2016). Interestingly, ROS, at low level, plays a positive role as signaling molecules and provides cross tolerance (Saxena et al. 2016).

Halophytes are important plant species which are effective materials to learn salt-induced oxidative stress tolerance. Moreover, these species show a higher productivity than glycophyte species under saline conditions (Bose et al. 2014). In many glycophytes, oxidative stress markers like MDA significantly increased only upon exposure to 50 mM NaCl. In contrary, many halophytes start increasing MDA level in shoots only above 150 mM (Ozgur et al. 2013) which happens mainly due to the higher antioxidant capacity of halophytes compared with glycophytes. While studying comparative salt tolerance in two coexistent glycophytes and halophytes, Radyukina et al. (2007) observed that extreme halophyte *Thellungiella halophila* showed higher constitutive levels of all three peroxidases as compared with the glycophytic *P. major* plants. The constitutive SOD levels in both roots and leaves of *P. major* were two to three times higher than in *T. halophila*. While comparing with *Pisum sativum*, SOD activity was found to be 10- to 40-fold higher in *Rhizophora stylosa* and *R. mangle* which provided very efficient antioxidant defense (Cheeseman et al. 1997). Seckin et al. (2010) investigated the differences in antioxidant defense system in two *Hordeum* species (salt-sensitive *H. vulgare* and halophyte *H. marinum*). They reported no variations of CAT, POX, and APX activities in H. vulgare and a decrease in SOD and GR activities at 300 mM NaCl, whereas in the halophyte species (*H. marinum*), there was a significant increase in the activities of all antioxidant enzymes compared to the control (Seckin et al. 2010). Apart from halophytes glycophytes also showed differences in their capacity in antioxidant defense system as reported in many plant studies. Different approaches in enhancing antioxidant defense system indicated plant's higher ability to maintain ion homeostasis, growth, and yield of plants (Hasanuzzaman et al. 2013; Table 18.5).

18.8 Conclusion and Future Perspectives

Salinity is an important abiotic stress that limits growth and yield of many crop species. The process of nutrient uptake by plants is disturbed under saline conditions since there is an antagonism between Na^+ and K^+ and/or Ca^{2+} and an antagonism between Cl^- and other anions resulting all of this in changes in the homeostasis within the plant. Disruption of ion homeostasis under salinity also caused oxidative stress in plants. In recent times dual role of ROS has been widely studied. Therefore, understanding the real-time changes in ROS production and metabolism would help in understanding the possible mechanisms. Learning from halophytes' salt tolerance mechanisms and using these traits in developing salt-tolerant glycophytes are the future tasks for plant biologists. The main process to achieve this knowledge is the improvement in several topics such as molecular genetics, functional genomics, proteomics, and metabolomic analyses as well as how these determinations affect in the salt tolerance of each species. Also, progressive studies have shown that combination of metabolic fluxes and physiological changes of plants provide accurate predictions about possible mechanism required for adaptation to stress.

Table 18.5 Summary of the protective effects of different exogenous protectants under salt stress

Name of the crop	Salinity dose and duration	Dose of protectant	Protective effects	References
Nicotiana tabacum BY-2 cells	200 mM, NaCl, 7 days	20 mM Pro	Enhanced the activities of POD and CAT	Hoque et al. (2007)
N. tabacum BY-2 cells	200 mM, NaCl, 7 days	20 mM GB	Increased the activity of POD	Hoque et al. (2007)
Cucumis melo L. cv. Yuhuang and cv. Xuemei	100 mM NaCl, 5 days	0.2 mM Pro	Reduced the $O_2^{\bullet -}$ level and the H_2O_2 content Enhanced activities of SOD, POD, APX, CAT, and DHAR	Yan et al. (2011)
Oryza sativa L. cv. KDML105	100 mM NaCl, 6 days	10 mM Pro	Decreased the activity of the antioxidant enzymes and upregulated the transcription of genes encoding several antioxidant enzymes	Nounjan et al. (2012)
Brassica juncea	NaCl 150 mM, 3 days	10 μM SA spray	Enhanced activities of CAT, POX, and SOD	Yusuf et al. (2012)
Zea mays L. cv. Partap-1	25, 50, and 75 mM NaCl, 30 days	10^{-8}, 10^{-6}, and 10^{-4} mM HBR, 12 h seed soaking	Enhanced antioxidant enzymes' activities and increased protein content Decreased lipid peroxidation	Arora et al. (2008)
Vigna sinensis	25, 50, 100, and 150 mM, 45 days	0.05 ppm brassinolide (2 sprays)	Increased antioxidant enzymes' activities Decreased lipid peroxidation	El-Mashad and Mohamed (2011)
Z. mays L. cv. DK 647	100 mM NaCl, 100 days	1 or 2 mM IAA (spray)	Reduced Na^+ concentration Increased those of Ca^{2+} and K^+ Increase Chl *a* and Chl *b* content Decreased electrolyte leakage and Pro content	Kaya et al. (2009)

(continued)

Table 18.5 (continued)

Name of the crop	Salinity dose and duration	Dose of protectant	Protective effects	References
Saccharum sp. cv. HSF 240	100, 120, and 140 mM NaCl, 30 days	0.5 mM AsA, 24 h	Increased activities of antioxidant enzymes Increased soluble protein contents	Munir and Aftab (2011)
Triticum aestivum L. cv. Giza 168	0.12%, 0.35%, and 0.70% NaCl, 65 days	α-Tocopherol 100 mg L^{-1} (spray)	Increased antioxidant enzymes' activities Decreased the levels of H_2O_2 and lipid peroxidation	Farouk (2011)
T. aestivum L. cv. Pradip	150, and 300 mM NaCl, 4 days	1 mM SNP, 1 day	Increased the content of nonenzymatic antioxidant Enhanced the activities of antioxidant enzymes Decreased lipid peroxidation	Hasanuzzaman et al. (2011b)
Citrus karna Raf.	3.0 dS m^{-1}, 90 days	50 mg L^{-1} Put	Improved the activities of SOD and POD Increased Pro content	Sharma et al. (2011)
O. sativa L. cvs. M-1-48, Nonabokra and Gobindobhog	200 mM NaCl, 15 days	1 mM Spd or 1 mM Spm, 15 days	Decreased MDA and H_2O_2 levels Increased antioxidant metabolism	Roychoudhury et al. (2011)
C. sativus	2000 ppm NaCl, 7 days	1 ppm Se, 14 days	Increased activities of POD, CAT, SOD, APX Reduction in reduction in electrolyte leakage and MDA content	Walaa et al. (2010)
B. napus L. cv. BINA Sharisha 3	100 and 200 mM NaCl	25 µM Na2SeO4, 48 h	Improved antioxidative capacity Decreased MDA and H_2O_2 levels	Hasanuzzaman et al. (2011a)
B. napus L. cv. BINA Sharisha 3	100 and 200 mM NaCl, 48 h	1 mM SiO_2, 48 h	Enhanced antioxidative defense Decreased MDA and H_2O_2 levels	Hasanuzzaman and Fujita (2011)

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Chapter 19
Salinity Stress Alleviation by Organic and Inorganic Fertilization

Nusrat Jabeen

Abstract Salinity is one of the major environmental stresses that limit plant growth and decreases crop production of more than 20% of irrigated land worldwide. The salinity reduced growth, yield, biomass, and quality of crop plants. These adverse effects are due to nutritional disorder induced by salinity which effects on the uptake, transport, and partitioning of nutrients within the plant. It is a need and demand of a time to develop an effective nutrient management package through different resources for the crops to promote growth, quality, and productivity under salt stress. This chapter reviews how to improve the nutritional status of the crop to enhance plant performance grown under salinity stress through different approaches. These different approaches include the use of organic fertilizer as soil amendments and the provision of inorganic fertilizer through foliar spray. Their beneficial effects are emphasized for the alleviation of salt stress on plant growth and productivity. These approaches could help to extend the threshold value of the crop grown in the soil which is considered nonproductive for cultivation due to higher levels of salinity.

Keywords Abiotic stress · Nutrient use efficiency · Organic agriculture · Plant nutrients · Soil fertility

19.1 Introduction

Among all environmental stresses, salt stress in soil is one of the major stresses, is always found to be harmful for the plants, and severely limits plant growth and its productivity (Paul 2012). Soil salinization severely degrades land of arid and semiarid areas where due to insufficient rainfall leaching of soluble salt from the soil and surface or internal soil drainage becomes restricted. It is a threat to agriculture as it has affected and continues to affect the land on which crops are, or might be, grown (Munns 2002; Parvaiz and Satyawati 2008). The use of brackish or saline water for

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irrigation on irrigated land can also cause salinity. According to the FAO (2005), 2% of agriculture land is salt affected, and about 20% of the world's cultivated area and nearly half of the world's irrigated lands are affected by salinity (Cheong and Yun 2007). Increased salinization of arable land might result 30% land loss within the next 25 years and up to 50% by the middle of twenty-first century (Wang et al. 2003).

Due to the diversity in the salt tolerance of various cultivated and non-cultivated plant species, they have been classified as glycophytes that can grow at less than 300 mM NaCl or halophytes which can survive on high concentrations of salt in the rhizosphere and grow well at more than 400 mM concentration of NaCl (Porcel et al. 2012; Shrivastava and Kumar 2015). Usually the yield of most crop plants under salt stress is reduced when the electrical conductivity (EC) of the saturation extract (EC_e) in the root zone of saline soil exceeds 4 dS m^{-1} (approximately 40 mM NaCl) at 25 °C and has an exchangeable sodium of 15%, though many crops show yield reduction at lower EC_e (Munns 2005; Jamil et al. 2011). Ions most commonly associated with soil salinity include the anions chloride (Cl^-), sulfate (SO_4^{2-}), carbonate(CO_3^{2-}), bicarbonate (HCO_3^-), and sometimes nitrate (NO_3^-) and the cations sodium (Na^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), and sometimes potassium (K^+) (Khaled and Fawy 2011).

Usually there is no single way to achieve a control on salinity in irrigated lands and associated water. An appropriate combination of different approaches and practices depending upon economic, climatic, social, as well as edaphic and hydrogeological situations is needed to manage salinity level within limits to commensurate with sustained crop productivity.

The use of salt-tolerant plant on saline soil has not been successful due to the differences in plant response to salinity stress in different ways and the variations in stresses. Selection of the plant species for providing economical yield under salinity depends upon the range of saline soil or saline irrigation water and edaphic and environmental factors. The method of transference of salt tolerance to the target species has also been reported unsuccessful by Sairam and Tyagi (2004). The additional yield of crops seems not possible even from water and soil management practices under salinity (Zahir et al. 2008).

The new technologies of combating salinity are under consideration, which must be more effective and less costly to maintain the flow of food, fiber, and industrial products. The rapid increase in population causes food and feed shortages around the world. Farmers and researchers are developing different cultural practices and techniques for sustained plant production to meet the requirements and effective tools to facilitate agricultural production in vast arid areas and lands. They are looking into the provision of essential macro-/micronutrient through soil amendment with organic fertilizer and foliar spray for plant growth promotion under salt stress.

Organic fertilization has been reported as an effective stress alleviation tool in crops. Organic materials, such as farmyard manures, agro-industrial by-products, composts, biogas slurry, etc., can be converted into nutrient-rich bio-fertilizer for sustainable land restoration practices (Suthar 2009; Jabeen and Ahmad 2017; Diacono and Montemurro 2010). Due to the presence of high organic matter in these organic fertilizers, it can be used for the remediation of salt-affected soil and as soil amendments to increase the soil fertility. Selected studies are there to focus on the effects of application of organic matter to salt-stressed soils, but the findings of researchers prove the potential of organic fertilizers in improving soil properties to increase biological productivity (Tejada et al. 2006; Walker and Bernal 2008; Cha-um and Kirdmanee 2011; Oo et al. 2013; Wang et al. 2014).

Absorption of nutrients through the leaves has been observed in various plants when applied on shoots. Application of macro- or micronutrients through foliar spray could partially offset the negative effect of NaCl on nutrient uptake by improving root growth which results in the uptake of nutrient by roots and thus prevents the nutritional disorder (Alpaslan et al. 1999; Rahman et al. 2015). Several research reports have provided evidence for the notion that foliar spray of micro- or macronutrients for increasing the plant tolerance is one of the best approaches to minimize the harmful effect of salinity by alleviating Na^+ and Cl^- injury to plants (El-Fouly et al. 2002; Akram et al. 2007; Tabatabaei and Fakhrzad 2008; Azeem and Ahmad 2011; Jabeen and Ahmad 2012a, b, c; Babar et al. 2014).

The purpose of this chapter is to provide a comprehensive analysis of scientific research on the changes in nutritional status, growth, and yield of the plants when treated with inorganic and organic fertilizer through different techniques under saline stress.

19.2 Organic Fertilization

Around 20% of the world's cultivated land is affected with salinity (Sumner 2000; Oo et al. 2013). Salt causes degradation of the soil structure which can affect water and air movement, plant-available water-holding capacity, penetration of root, seedling emergence, overflow and erosion, tillage, and sowing processes. Salinity disrupts soil pH, cation exchange capacity (CEC), exchangeable sodium percentage (ESP), and organic carbon and also brings change in the osmotic and matric potential of the soil solution (Wang et al. 2014) which causes deficiencies and imbalances in plant nutrients (Mengel and Kirkby 2001). It also adversely affects soil microbial communities and their activities (Rietz and Haynes 2003).

Organic matter has several beneficial effects on agricultural fields. When used as soil amendments, it releases nutrients slowly, maintains structural stability of soil, protects soils against erosion, and improves physical, chemical, and biological properties to increase the overall soil fertility (Diacono and Montemurro 2010, 2015). To reclaim the salt-affected soil, the application of organic matter (farmyard manure, compost, vermicompost, green manure, organic amendments, municipal solid waste, etc.) has become a common practice worldwide in the cation exchange capacity last several decades and constitutes an important method of soil regeneration and fertility enhancement under salinity (Mitchell et al. 2000; Hanay et al. 2004; Sharma and Minhas 2005; Tejada et al. 2006; Melero et al. 2007; Wang et al. 2014; Jabeen and Ahmad 2017). Some selected findings are summarized in Table 19.1 to show the effects of application of different organic materials on different crop plants under different levels of salt-stressed soils.

Table 19.1 Effects of various organic fertilizers on crop productivity under salinity (some selective data)

Organic materials	Salinity levels	Effects on crop plants	References
Cotton gin crushed compost and poultry manure	ECe 9.1 dS/m pH 8.0	The percentage of spontaneous vegetation (*Artemisia herba-alba, Moricandia arvensis, Plantago albicans* being the most abundant) cover >50% in all treated plots and 8% in the control soil. Affect positively the soils physical and chemical properties, soil microbial biomass, and six soil enzymatic activities	Tejada et al. (2006)
Compost (produced from by-products of the olive oil industry) and poultry manure	ECe1.85 dS/m pH 7.7	Soil amendment with compost and manure increases markedly the shoot growth of *Beta maritima* L. (sea beet) and *Beta vulgaris* L. (sugar beet) plant. Increases soluble and exchangeable-K^+ (thus limiting the entry of Na^+ into the exchange complex)	Walker and Bernal (2008)
Green manure mixed with farmyard manure	1–2% salt ECe 8.4–20.4 dS/m pH 4.58–4.79	The remediation of salt-affected soil in paddy fields using organic manure is as an effective way of enhancing rice food crop productivity	Cha-um and Kirdmanee (2011)
Gypsum and farmyard manure	ECe 12.5 dS/m pH 5.16	Gypsum and farmyard manure treatment provide an effective remedy to ameliorate salinity, result in decrease of sodium ions in jasmine rice with the yield improvement	Cha-um et al. (2011)
Compost (animal wastes and plant residues)	ECe 4.03–5.11 dS/m pH 8.62–8.75	Organic amendments co-applied with chemical amendments reduce soil pH, salinity, and sodicity. It shows highest sodium removal efficiency with highest biomass yield of alfalfa	Mahdy (2011)
Cassava-industrial waste compost and vermicompost with/without earthworms	ECe 4.26 dS/m pH 7.30	Organic amendments decrease ECe, improve maize crop growth via improving availability of essential mineral nutrients	Oo et al. (2013)
Green waste compost (GWC), sedge peat (SP), and furfural residue (FR) and its mixture	ECe 3.69 pH 7.75	The combination of GWC, SP, and FR (the GSF treatment) provides better remediation results than each applied singly and has substantial potential for ameliorating saline soils and promotes Pagoda tree (*Sophora japonica*) growth. Increase total porosity and organic carbon of soil	Wang et al. (2014)

(continued)

Table 19.1 (continued)

Organic materials	Salinity levels	Effects on crop plants	References
Soil amendment with compost at two rates (5 and 10 ton fed^{-1}) in combination with three rates of N fertilization (35, 50, and 70 kg N fed^{-1})	ECe 20.5 dS/m pH 8.5	Compost serves as soil conditioner and improves soil physical and chemical properties. Increase nutrient uptake and yield of rice crop under 70 kg N fed^{-1} and 10 ton compost fed^{-1}	Zaki (2016)
Vermicompost and biogas slurry	ECe 9.9 dS/m pH 8.8	Soil amendments show better result even at high salinity level (ECe 9.9 ds/m) on the growth and N assimilation in sunflower. Increase the availability of nitrogen and other minerals to the crop	Jabeen and Ahmad (2017)
Organo-mineral fertilizer (OMF) compost	ECe 6.73 dS/m pH 7.79	Application of OMF compost at a rate of 20 ton h^{-1}, as an alternative to 50% of the recommended dose of mineral-NPK fertilizers, improve the soil chemical and physical properties. This treatment also improves sustainable agronomic performance of common bean	Rady et al. (2016)
Composted organic fertilizers (poultry and cow manures)	ECe 6.5 dS/m	Composted organic fertilizers (poultry and cow manures) increase nodulation, productivity, and forage quality of *Clitoria ternatea* L. than inorganic fertilizer (NPK) under saline condition in arid lands	Abusuwar (2017)

19.2.1 Effects of Organic Fertilizer on Soil Physical Properties

Organic matters improve soil aggregate stability by a reduction of soil sodicity. Ca^{2+} in composts could decrease the proportion of Na^{+} in the exchange complex and accelerate the leaching of exchanged Na^{+} (Qadir and Oster 2004). Organic amendments control the erosion in saline soils and improve the flocculation of clay minerals and formation of soil aggregates. The aggregate stability improves the physical properties of soil such as porosity, water infiltration, and water-holding capacity, thus minimizing the effect of drought (Oo et al. 2013). According to Hussain et al. (2001), amendment of sulfuric acid, gypsum, farmyard manure, and their various combinations in soil could decrease sodium adsorption ratio of the soil significantly. A direct correlation was found between organic matter additions and decreased soil bulk density and increased total porosity which improve saline water leaching (Kahlown and Azam 2003; Tejada et al. 2006; Wang et al. 2014).

19.2.2 Effects of Organic Fertilizer on Soil Chemical Properties

The uptake of macronutrient, phosphorous (P), can be reduced in saline soils, and organic acid releases humic substances during mineralization process which convert soil phosphate into available forms (Hu and Schmidhalter 2005; Lakhdar et al. 2009). Under saline soils organic matter content can increase the available fraction of potassium (K^+) through the increase of cation exchange capacity (CEC). K^+ helps in maintaining the turgor pressure of plant under salinity stress. The soil amendments with poultry manure and compost can increase both the CEC and the soluble and exchangeable-K^+, thus, limiting the entry of Na^+ into the exchange complex (Walker and Bernal 2008). Wang et al. (2014) showed that a mixture of green waste compost, sedge peat, and furfural residue (1:1:1 by volume) significantly reduced Na^+/K^+ content and improved CEC and available form of N, P, and K content. Some studies suggested that some livestock manure contains significant amount of salt and their continued application may result in an accumulation of salt in agricultural land soil (Hao and Chang 2003; Li-Xian et al. 2007). Therefore selection of organic fertilizers as nutrient sources, timing, and method of its application are very important (Diacono and Montemurro 2010; Khaled and Fawy 2011).

19.2.3 Effects of Organic Fertilizer on Soil Biological Properties

The effects of salinity on soil chemical and physical properties and on plant growth are well documented (Keren 2000), whereas soil biological properties in saline environments have not been studied extensively (Rietz and Haynes 2003). Diacono and Montemurro (2015) reported that exogenous organic matter applications to cropland improve soil biological functions and positively affect salt-affected soils. Salinization adversely affects large variety of microbial mediated processes in soil. It has been demonstrated that incorporation of organic manure significantly stimulate urease, alkaline phosphatase activity and respiration rate in soil derived from alluvial and marine deposits with 3.3 $g \cdot kg^{-1}$ total salts (Liang et al. 2003). Some authors reported that the C/N ratio plays an important role in the decomposition of organic matter by microorganism. Both increases and decreases in C or N mineralization depend upon increasing salinity as Chandra et al. (2002) found that application of low concentration of salts stimulated carbon mineralization, but high concentration of salts had a toxic effect on microorganism activities. Carbon and nitrogen mineralization in saline soil respond according to the type of organic material applied to the soil (Walpola and Arunakumara 2010). Liang et al. (2005) confirm that salinity-induced toxicity can be minimized by saline soil amendment with organic manure which can be an economical and cost-effective method. They found that rice straw in combination with pig manure had higher significant effects on enzymatic and microbial activity in salt-affected soil than rice straw and manure alone. Furthermore, it has also been demonstrated by Tejada et al. (2006) that application of non-composted and compost manure to a saline soil in dryland can reduce exchangeable sodium percentage by 50% than unamended soil and significantly increase different enzyme activities, i.e., urease, alkaline phosphatase, and dehydrogenase. Moreover, Rao and Pathak (1996) found that green manure amendment increased urease activity of saline and alkali soils and enhanced microbial activity at EC $\leq$26 salinity level.

It can be concluded that an appropriate use of organic amendments could be an effective measure to reclaim salt-affected soils for a better crop yield.

19.3 Foliar Fertilization

Foliar fertilization is an effective method of supplying of nutrients, plant hormones, stimulants, and other beneficial substances, in combination with some traditional root fertilization to achieve a balance of nutrients in plants. The macro- and micronutrients are the basic need of crop plants.

The crop plant can easily get macronutrients C, H, and O from air and water. The remaining nutrients, i.e., N, P, K, Ca, Mg, and S, and micronutrients, i.e., Zn, Cu, Fe, Mn, B, Mo, Cl, and Ni, must be present in adequate amount and proportion in the plant growth medium to fulfill the requirement of plants to complete its life cycle (Fageria et al. 2008). Soil application is the traditional method to supply water-soluble essential nutrients with fertilizers to plants which are absorbed by plant roots. Sometime nutrients are not easily available by the plant roots as they are strongly fixed by soils. For example, iron in calcareous soil cannot be absorbed by plant roots and plants become deficient of iron. The deficiency of iron can be corrected efficiently by the foliar application of ferrous sulfate or iron chelates solution (Fageria et al. 2008).

Though higher plants can also absorb mineral nutrients through foliar sprays, in high-yielding cultivars, nutritional requirements, in particular macronutrient, are rarely met with foliar applications. Plant response to foliar fertilization is dependent on species, fertilizer form, its concentration, frequency of application, and the plant growth stage. Foliar applications are scheduled in such a way to meet the demand of nutrients at vegetative or fruiting stages of growth, and fertilizer formula is adjusted according to need (Haytova 2013).

These applications may help plants recovering from any damaging environmental conditions, e.g., transplant shock, hail damage, drought, salinity, etc. Nutrient uptake through the root system in crops growing under saline environment is restricted due to salt stress, and foliar application has been proved to be an effective method to correct nutritional disorder. Provision of nutrients through foliar application alleviates the negative effect of stress influencing root growth and absorption capacity (El-Fouly and Abou El-Nour 1998; Hussein et al. 2012; Jabeen and Ahmad 2012a, b, c; Jabeen et al. 2013).

With the advantages of foliar spray, there are some disadvantages as well. It has been experienced by some authors that in favorable climatic conditions, crop plant takes at least 5–6 days to respond toward soil-applied fertilizer. It has long influence on plant growth. However a crop plant responds in 3–4 days to foliar application of nutrients and it is often only temporary. This means several foliar applications are necessary to meet nutrients requirements. The repeated application of foliar spray may also due to constant loss of leaf blades to mowing. Leaf area of plants must be sufficient for the absorption, and due to leaf damage by high nutrient concentrations, very low dose can be applied**.** Nutrients, applied to the foliage, have to penetrate barriers, i.e., the waxy cuticle covering, cell wall, and plasma membrane of the epidermal cells. So that the morphology and organization of leaf tissue must be like that, it absorbs the gaseous plant nutrients. Regardless of these drawbacks others proved foliar fertilization, a very economical and efficient way of fertilization to supplement the plants' nutrients (Girma et al. 2007). Foliar sprays must be practiced at the "critical stages" of plant growth cycle and must be applied during or shortly before the critical period to be effective (Jabeen and Ahmad 2012a, b, c). Time schedule must be in one's mind for foliar spray. Morning application is considered to be very suitable as there is less evaporation in morning thus giving a better chance for maximum absorption of nutrients by leaves (Jabeen and Ahmad 2012a, b, c). According to Fageria et al. (2008), the best time for foliar fertilization is after 2–3 PM when stomata are opened and air temperature is low because high temperature can cause burning of plants. High relative humidity is directly related with high rates of foliar uptake. In low humidity rapid drying can cause crystallization of minerals on the leaf surface (Gamble and Emino 1987). Foliar fertilization must not be practiced in windy days as it can drift the spray solution. After application of nutrients, there must not be rain for at least 3–4 h as applied nutrients take 3–4 h to be absorbed by the plant leaves. Addition of surfactant, i.e., sticky material, in nutrient solution is necessary to stick the spray drops on plant leaves. Surfactant helps in penetration of the nutrient solution. Another important factor for foliar spray is pH of spray solution. It has been observed by Kanan (1980) that most suitable range of pH values are 3.0–5.5 for the maximum uptake of mineral nutrients. A moderate acidic medium of spray solution can help nutrients to penetrate leaf surfaces effectively.

19.3.1 Mechanisms of Uptake of Foliar-Applied Nutrients

There are sufficient evidences which prove the absorption of inorganic and organic material through leaves surface. It may be different from the roots absorption as root cell walls lack cuticle. Earlier research showed that foliar-applied nutrients first penetrate the cuticle and the cell wall through diffusion and then are adsorbed to plasma membrane and at last the absorbed nutrients are taken up into the cytoplasm (Franke 1967). Later it was proved that foliar absorption is easier when leaves' stomata are open (Eichert and Burkhardt 2001). The penetration of ions depends on the kind of charge, adsorbability, and ion radius. The light quality and intensity may help to increase ion absorption by leaves (Fageria et al. 2008).

The mobility of the nutrient throughout the plant is important for the development of plants. Foliar-applied nutrients move freely with water stream, but some nutrients show immobility and become restricted to phloem. This restriction of nutrients does not show positive effects of foliar application and plants show deficiency symptoms (Papadakis et al. 2007).

Macronutrients show high mobility in plant tissues, except calcium and sulfur. Calcium when taken up by leaves cannot move with water stream freely and fail to reach younger tissues or fruits where it may be required (Fageria et al. 2008). Potassium and nitrogen show high mobility when applied on leaves. They rapidly distribute throughout the plant tissues and produce promising results of plant growth even under saline conditions (Ahmad and Jabeen 2005; Jabeen and Ahmed 2011a, b, 2012a, b, c).

Micronutrient requirements can meet by foliar application which is more uniform than soil application. It is required in traces for plant growth. Most of the micronutrients mobility in plant tissues is reported to be poor. According to Marschner (1995), Fe may show low and Mn show intermediate mobility in the plant phloem. Garnett and Graham (2005) found much higher reproductive mobility of Fe in wheat than Mn. Therefore, it can be concluded that differences exist among nutrients and plant species in remobilization in plant tissues. Foliar spray of micronutrients on plants grown under salinity stressed can offset adverse effect of salinity by improving growth and nutrient status of plants. Abou El-Nour (2002) reported a significant increase in root dry weight of maize crop sprayed with EDTA micronutrient compound under salinity. Jabeen and Ahmad (2011b) found improvement in growth and biochemical activities when applied B and Mn on foliage of sunflower under non-saline or saline conditions. Thus it can be manipulated that nutrient correction may be possible by foliar fertilization when crop plants face stress or when soil-applied nutrients are ineffective due to immobility (Fageria et al. 2008).

The source and concentrations of macro and micronutrients major salts generally used for foliar spray are presented in Table 19.2.

19.4 Salinity Effects on Plants

Salinity causes both ionic and osmotic stress in major crop plants and Na^+ is the primary case of ion-specific damage. The presence of high concentration of Na^+ in the soil can alter the basic soil texture resulting in decreased soil porosity and thus reduced soil aeration and water conductance. Due to the low water potential in root zone, plant cannot acquire water and nutrients which results in decreased plant productivity (Munns and Tester 2008). Plant response under stress is species and genotype dependent and depends on the length and severity of the salinity, the age and stage of development, the organ and the cell type, and the subcellular compartment (Parvaiz and Satyawati 2008). The onset and development of salt stress within a plant result in the reduction in the growth, whole plant mechanism contributes to avoid the stress throughout the life cycle, but growth can resume as stress is relieved (Parida and Das 2005).

Table 19.2 Source and concentrations of macro- and micronutrients major salts generally used for foliar spray to correct deficiencies

Nutrient	Common name	Formula	Element (%)	Concentration (Kg/500 L of water)
N	Urea	$CO\ (NH_2)_2$	46	3–5
N	Ammonium sulfate	$(NH_4)_2SO_4$	21	2–3
	Ammonium nitrate	NH_4NO_3	35	
	Diammonium phosphate	$(NH_4)_2HPO_4$	18	
	Ammonium chloride	NH_4Cl	26	
	Monoammonium phosphate	$NH_4H_2PO_4$	11	
P	Phosphoric acid	H_3PO_4; others see N above	55	2–3
K	Potassium chloride	KCl	60	1.5–2.5
	Potassium nitrate	KNO_3	44	
	Potassium sulfate	K_2SO_4	50	
Ca	Calcium chloride	$CaCl_2$	36	1.5–2.5
	Calcium nitrate	$Ca(NO_3)_2$	16	
Mg	Magnesium sulfate	$MgSO_4$	20	3–10
	Magnesium nitrate	$Mg(NO_3)_2$	16	
Fe	Ferrous sulfate	$FeSO_4.H_2O$	33	3–6
Mn	Manganese sulfate	$MnSO_4$	23–28	1–2
Zn	Zinc sulfate	$ZnSO_4.H_2O$	36	1.5–2.5
Cu	Copper sulfate	$CuSO_{4.}H_2O$	35	0.5–1
B	Sodium borate; boric acid	$Na_2B_4O_7$; $H_3BO_3[B(OH)_3]$	20;17	0.25–0.5
Mo	Sodium molybdate	$Na_2MoO_{24}.2H_2O$	39	0.1–0.15

Source: Adapted from Fageria et al. (2009)

Salinity effects are the results of complex interactions of plant metabolic activities such as seed germination, growth, and water and nutrient uptake (Singh and Chatrath 2001; Akbarimoghaddam et al. 2011). Plants growing in saline soil face three different physiological stresses. First, the toxic effects of sodium and chloride disrupt enzyme structure, and other macromolecules cause severe ion deficiencies which result in cell damage and reduction in leaf area, chlorophyll content, stomatal conductance, and respiration and inhibit protein synthesis (Netondo et al. 2004). Second, plant when exposed to the low osmotic potentials of saline soil has to maintain lower internal osmotic potentials to stop exosmosis; failure of the osmotic balance can lead to cell dehydration. Finally salinity also upset the nutrient balance and produces nutrient (N, Ca, K, P, Fe, Zn) imbalance in the plant due to decreased nutrient uptake to the shoot (Evelin et al. 2009; Porcel et al. 2012). Ion toxicity is the result of replacement of potassium (K) by sodium (Na) in biochemical reactions, and sodium (Na) and chlorine (Cl) bring changes in synthesis of proteins. Potassium acts as a cofactor for several enzymes, and its high concentration is also required for the binding of tRNA to ribosomes for protein synthesis (Zhu 2002). Salinity also reduces uptake of phosphorus (P) in plants because in saline soil phosphate ions precipitate with calcium (Ca) ions (Bano and Fatima 2009). Due to ion toxicity and osmotic stress, metabolic imbalances lead to oxidative stress in plants (Chinnusamy et al. 2006). The saline growth media also adversely affect development of crop plants during the reproductive phase by inhibiting microsporogenesis and stamen filament elongation and lead to apoptosis in some tissues, ovule abortion, and senescence of fertilized embryos, hence reducing crop yield (Shrivastava and Kumar 2015).

It can be concluded that salt stress affects all the major metabolic processes and brings changes in nutritional status which leads to alter biochemistry and physiology of the plants and ultimately reduce its growth and yield.

19.5 Salinity Stress Alleviation

There must be alternative approaches for alleviation of salinity to maximize the plant growth. Reclamation of salt-affected soils such as scraping, flushing, and leaching was found to be very expensive. The change in farming management practices can be a good approach, but its implementation is often limited because of cost and lack of good-quality water or water resources. Conventional plant breeding methods to improve salt tolerance are time-consuming and laborious and depended on existing genetic variability. Development of easily adaptable methods which must be efficient and low in cost for the stress management is a worldwide challenge. Researches are being carried out to develop strategies to cope with the salinity stress. The amendment of soil with organic matter and foliar feeding of nutrients could be the better approach and effective tools for the alleviation of salinity stress during the growth cycle of plants (Jabeen and Ahmad 2017; Yildirim et al. 2009).

Now we will discuss the alleviating effect of organic amendment and foliar spray on major metabolic processes of crop plants under salinity stress.

19.5.1 Alleviating Effect of Organic Amendment and Foliar Spray on Major Metabolic Processes of Crop Plants Under Salinity Stress

19.5.1.1 Growth and Development

The soil salinity or irrigation with saline water depresses all growth parameters of the plants. The reduced crop growth under saline rooting medium may be due to failure of the osmotic balance which causes reduction in turgor pressure of expanding tissues and reduction in photosystem activity and ability to produce and utilize assimilates to the growing regions (Jabeen and Ahmed 2012a, b, c).

A significant increase in growth of sunflower (plant height, leaf area, stem and disc diameter, fresh and dry biomass) was well demonstrated due to application of organic manure (vermicompost and biogas slurry) under salinity (Table 19.3). The application of organic fertilizer has not only overcome sodium-induced toxicity of

Table 19.3 Effect of organic manure on growth parameters and biomass of sunflower under different salinity levels

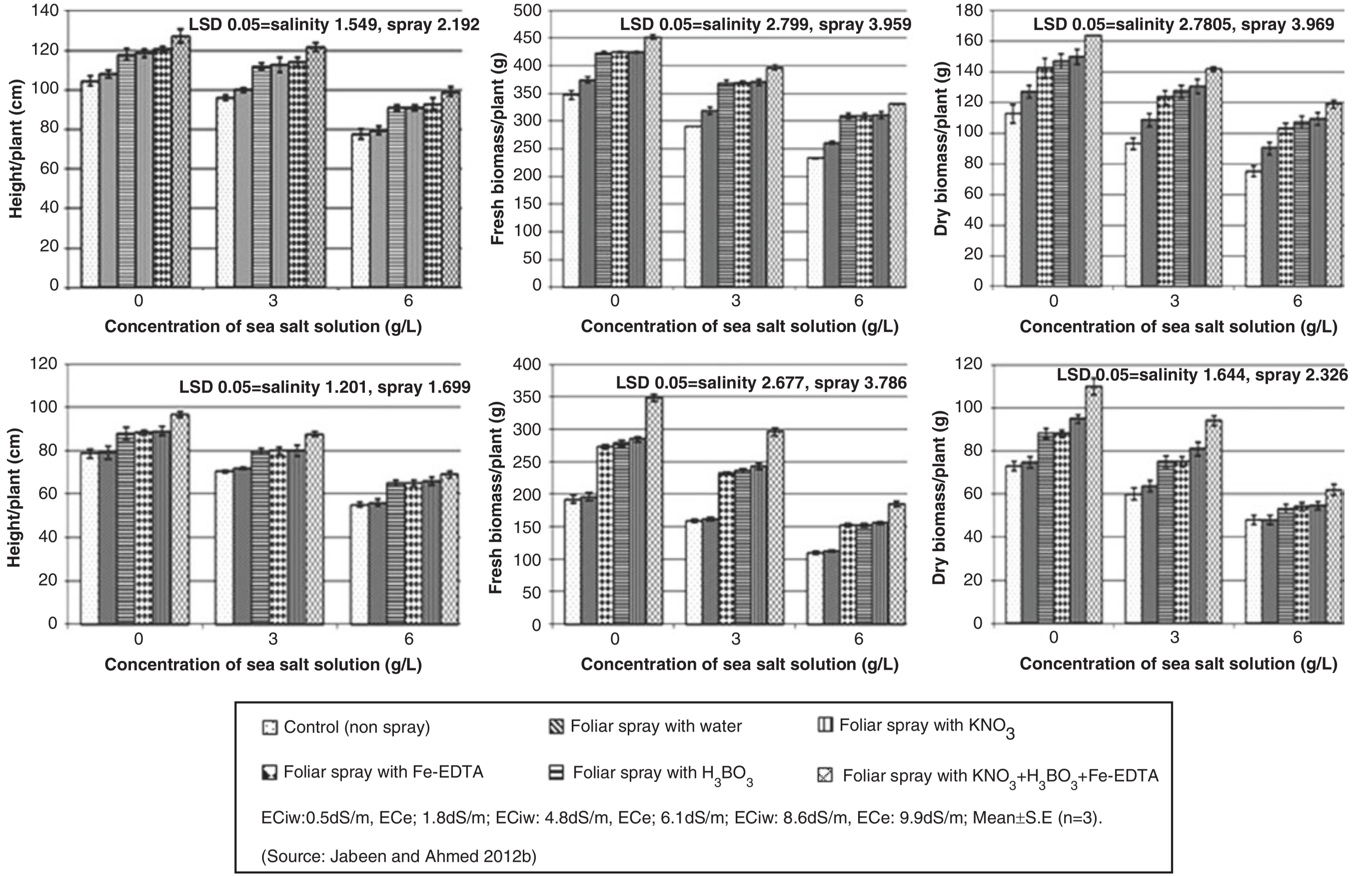
Sea salt concentration (g/L)	Organic manure	Plant height (cm)	Stem diameter (cm^2)	Leaf area (cm^2)	Diameter of floral disc (cm)	Total fresh biomass (gm)	Total dry biomass (gm)
0 ECiw 0.5 dS/m, ECe1.8 dS/m	C	104.00 ± 2.31	0.795 ± 0.058	115.52 ± 2.60	10.00 ± 1.15	346.50 ± 4.19	83.37 ± 7.16
	BGS	123.00 ± 1.73	1.127 ± 0.002	140.02 ± 2.31	9.25 ± 0.43	335.25 ± 11.09	95.50 ± 3.23
	VC	126.17 ± 2.32	1.179 ± 0.051	208.07 ± 4.62	11.35 ± 0.49	487.00 ± 1.22	144.90 ± 3.12
	BGS+VC	129.17 ± 2.32	1.265 ± 0.018	229.97 ± 4.62	12.25 ± 0.17	555.78 ± 4.20	178.90 ± 8.83
3 ECiw 4.8 dS/m, ECe 5.9 dS/m	C	92.17 ± 1.74	0.827 ± 0.058	92.53 ± 2.02	7.28 ± 0.52	213.35 ± 8.05	52.25 ± 1.73
	BGS	99.17 ± 2.32	0.885 ± 0.079	90.90 ± 6.35	8.90 ± 0.98	269.60 ± 2.05	74.47 ± 6.55
	VC	102.17 ± 1.74	1.080 ± 0.058	110.44 ± 1.44	11.00 ± 1.15	364.95 ± 5.50	100.65 ± 0.97
	BGS+VC	109.00 ± 4.04	1.079 ± 0.052	138.50 ± 3.18	10.00 ± 0.69	352.04 ± 3.99	92.35 ± 8.69
6 ECiw 8.6 dS/m, ECe:9.8 dS/m	C	77.17 ± 1.74	0.667 ± 0.03	61.33 ± 1.45	6.00 ± 0.46	110.38 ± 8.07	38.36 ± 1.74
	BGS	83.50 ± 2.60	0.897 ± 2.60	63.02 ± 2.31	7.00 ± 0.75	180.67 ± 0.43	53.10 ± 6.35
	VC	93.00 ± 1.73	1.042 ± 0.06	102.65 ± 1.45	10.50 ± 0.40	287.65 ± 8.05	78.93 ± 3.19
	BGS+VC	93.17 ± 1.74	1.043 ± 0.02	116.00 ± 2.31	9.40 ± 0.72	306.37 ± 2.32	81.51 ± 3.23

Source: Adapted from Ahmad and Jabeen (2009)
The values are mean ± SE ($n = 3$)
BGS Biogas slurry, *VC* Vermicompost

substrate but also helped in restoring growth up to certain extent. Recovery from sodium-induced toxicity by supplement of abovementioned organic fertilizer was comparatively more in plants irrigated with saline water having EC 4.8 dS/m, than those irrigated with saline water of EC 8.6 dS/m, due to higher salt content in the latter. This increase is due to the organic fertilizer amendment which improved the soil structure by increasing its water-holding capacity, aeration, and drainage. It also provides auxin, amino acids, and vitamins which are plant growth-influencing material produced by their decay (Ahmad and Jabeen 2009).

Significant increases in vegetative growth were also reported by Abou El-Magd et al. (2008) on sweet fennel, irrigated with saline well water (5000 ppm), and fertilized with poultry manure. Ahmad et al. (2009) also reported a promotion in growth vigor of ginger by the application of vermicompost and biogas slurry under non-saline condition which persisted even after encountering toxicity due to saline water irrigation. Inhibitory effect of saline water irrigation on number of shoots and their height, fresh and dry biomass of shoot, and fresh and dry weight of rhizome appeared to be removed under amendment of vermicompost up to greater extent and with mixture of biogas slurry up to lesser extent, whereas amendment of only biogas slurry showed growth-promotive effects only on rhizome production. The findings of Oo et al. (2013) suggested that the use of compost and vermicompost as soil conditioners could contribute to improve physical, chemical, and biological properties of the saline soil and increase its nutritive value for the growth of maize crop plants. Results obtained by Abdel-Ati and Eisa (2015) indicated that rice straw compost (RS-compost) and olive mill wastewater compost (OMW compost) had positive effects on soil properties and led to increase barley plant height and plant fresh and dry weight under salinity. Rady et al. (2016) observed growth improvement in common bean plants with increased application rate of organo-mineral fertilizer (OMF) compost which could be attributed to the enhanced decomposition of the OM and mineralization of nutrients.

The detrimental effects of salinity on growth could also be partially alleviated by the application of nutrient solution through decreasing the nutrient demand in salt-affected plants. El-Fouly et al. (2002) found improvement in growth and dry weight of tomato seedlings by the foliar application of a micronutrient compound containing 2.8% Fe +2.8% Zn +2.8% Mn at 1.5 ml/l, in response to the increased NaCl level in the root growth medium. Akram et al. (2009) observed an improvement in growth of sunflower due to the foliar spray of K^+ at 1.25% using different salt (KCl, KOH, K_2CO_3, KNO_3, KH_2PO_4, and K_2SO_4) under saline concentration of 150 mM NaCl. Foliar application of 10 mM KNO_3 and $Ca(NO_3)_2$ alleviated deleterious effects of salinity stress (40 mM) on strawberry growth and increased plant root and shoot dry weight by 50% (Yildirim et al. 2009). A significant increase in height and fresh and dry biomass was observed in sunflower and safflower plants when sprayed by individual macro- (K) or micronutrient solutions (B and Fe) using different salt (KNO_3 at 250 ppm, H_3BO_3 and Fe-EDTA at 5 ppm), but combined effects of their mixture were more significant irrespective to their growth under non-saline (ECe 1.8 dS/m) or saline conditions (ECe 6.1 and 9.9 dS/m) (Fig. 19.1a, b). The results suggested that foliar application could be used to correct the nutrients deficiency in stressed plants and improve its tolerance to salinity. Stimulating effects of these nutrients on metabolism, biological and enzyme activities encourage plant growth. Babar et al. (2014)



ECiw:0.5dS/m, ECe; 1.8dS/m; ECiw: 4.8dS/m, ECe; 6.1dS/m; ECiw: 8.6dS/m, ECe: 9.9dS/m; Mean±S.E (n=3).

(Source: Jabeen and Ahmed 2012b)

Fig. 19.1 Effect of salinity and foliar spray of water, potassium, iron, boron, and its mixture on (**a**) height and fresh and dry biomass of sunflower plant. On (**b**) height and fresh and dry biomass of safflower plant observed stimulatory effects on growth and biomass of fenugreek plants by the foliar application of salicylic acid (SA) under salt stress. Hussein and Alva (2014) reported a significant decrease in growth parameters of millet plants under high salinity level. Fifty-two percent decrease was recorded in total plant dry weight under 7.8 $dS \cdot m^{-1}$ salinity as compared to control. Foliar application of ascorbic acid with zinc sulfate significantly increased total plant dry biomass. Foliar application of Zinc has also been reported to increase plant growth and yield of peanuts (Darwish et al. 2002; Gobarah et al. 2006) and sunflower (Thalooth et al. 2005). Applying ZnSO4 at 30 ppm as a foliar application into barley plants increased the plant productivity as a result of enhancing the plant metabolism and growth (Abdel-Ati and Eisa 2015).

19.5.1.2 Ion Levels

Under salt stress conditions, elevated Na^+ disrupt the nutrient uptake by interfering with various transporters such as K^+-selective ion channels in the root plasma membrane and inhibit root growth by the osmotic effects on soil structure. Under salinity soils are frequently characterized by the ratio of Na/K, Na/Ca, and Cl/NO_3 that leads to plant nutrient deficiencies. Thus the uptake of water and all other essential mineral nutrients such as P, K, Fe, Cu, and Zn can be reduced in the roots and shoots with increasing salt concentration in the growth medium (Abou El-Nour and El-Fouly 2006; Porcel et al. 2012). Certain ion ratios, such as K/Na, are indicators for evaluation of salinity tolerance in plants, and high Na^+/K^+ ratio disrupts various metabolic processes in the cytoplasm (Tester and Davenport 2003).

Application of organic manure as fertilizer significantly decreased Na^+ and increased K^+ content in sunflower leaves, bract, and seed coat under saline water irrigation (Ahmad and Jabeen 2009). Abou El-Magd et al. (2008) also confirmed that application of organic manure increased the availability of K^+ content, nitrogen, and phosphorus to the whole sweet fennel plant. Cha-um et al. (2011) reported in root and leaf tissues of jasmine rice, grown in saline soil treated with gypsum and farmyard manure, lower sodium and higher potassium ion accumulation as compared to those grown in untreated saline soil.

The amendment of organo-mineral fertilizer (OMF) compost at 20 or 30 ton h^{-1} in saline soil reduced Na level significantly, but no significant effects were observed on the levels of N, P, K, and Ca in *Phaseolus vulgaris*. The highest significant values for the ratios of K:Na and Ca:Na were obtained with the application of 30 ton OMF compost h^{-1} (Rady et al. 2016). The OMF through slow release of nutrients into the soil or to plant improved soil properties and helped to overcome the nutrients loss by leaching processes. Zaki (2016) showed that the compost at a rate of 10 ton fed^{-1} with 70 kg N fed^{-1} increased nutrient uptake (i.e., N, P, K, Fe, Zn, and Mn) of rice straw and grain. Increasing nutrient uptake of rice straw and grain when bio-fertilizers and chicken manure were added with N fertilization levels in saline soil could be due to improvement in soil chemical and bio-properties. Bio- and organic fertilizer applications have also been reported to reduce the harmful effects of salinity (0%, 20%, and 40%) through reduction of Na ion accumulation in wheat. It increased the K/Na ratio in the tissues which is essential for survival in saline habitats (Al-Erwy et al. 2016).

It has been reported that provision of essential nutrients through foliar spray might offset the negative effect of salt on nutrient uptake to some extent through improving root growth. El-Fouly et al. (2002) found in tomato a gradual decrease in the uptake of all micro- and macronutrients with the increase of NaCl concentration (i.e., 1000–3000 ppm) in growing medium. Akram et al. (2007) found a decrease in N, P, K, Ca^{2+}, and Mg^{2+} in salt-stressed sunflower plants with the increasing concentrations of Na^+ and Cl^-. KOH at 0, 0.5, 1.0, 1.5, and 2.0% was applied as a foliar spray to salt-stressed and nonstressed sunflower. Application of K^+ increased K^+/Na^+ ratio of salt-stressed plants with the increase in growth and yield. The foliar application of 10 mM KNO_3, $Mg(NO_3)_2$, and $Ca(NO_3)_2$ on strawberry plant grown under salinity (40 mM) increased the concentration of N, K, Mg, Ca, S, P, Fe, Mn, Zn, and Cu content of both root and shoot with their respective control. The highest root (Na)/shoot(Na) and root(Cl)/shoot(Cl) ratio obtained from $Ca(NO_3)_2$ at 10 mM concentration indicates that Ca, K, and Mg transport was impaired by Na under saline conditions and could disturb plant metabolism and reduce plant growth (Yildirim et al. 2009). Asik et al. (2009) observed soil application of humus at 1 and 2 g/kg and foliar application of liquid humic acid at 0.1 and 0.2% under 15 and 60 mM saline conditions positively affect the nutrient uptake in wheat plant. Soil application of humus increased the N uptake, and foliar application of humic acid increased the uptake of P, K, Mg, Na, Cu, and Zn. Jabeen and Ahmad (2012b) found a decrease in K, Fe, and B and an increase in Na^+ content of sunflower and safflower plant leaves grown under salinity (4.8 dS/m and 8.6 dS/m). Foliar application of nutrient solution, i.e., KNO_{3+} H_3BO_{3+}Fe-EDTA, for K, B, and Fe increased element concentration by 20% compared to unsprayed leaves at 8.6 dS/m salinity.

Rashad and Hussien (2014) observed foliar application effects of 100 mg L^{-1} solution of gibberellic acid (GA3), salicylic acid (SA), and silicon on the nutritional content of the maize plant leaves (*Zea mays* L.). GA3 was found to be the most effective in reducing Fe, Zn, and Si toxicity due to the salinity effects on the leaves. Copper and manganese deficiency may be controlled but to a limited extent by SA and then by GA3. Both materials enhanced nitrogen content of the leaves and potassium to a lower extent. But sodium content as well as sodium/potassium ratio of the leaves was highly increased as affected by SA and GA3 and decreased by Si application. This may be due to formation of Na salts of both acids in the plant leaves. Silicon ions compete with sodium ions to reduce their absorption by the maize plants. According to Sadak et al. (2015), mineral ion concentration including N, P, K^+, Ca^{2+}, and Mg in the leaves of faba bean plants gradually decreased by increasing salinity levels (i.e., 3.13 and 6.25 dS m^{-1}). With the increase in Na^+ and Cl^- concentration of faba bean leaves, the K^+:Na^+ ratio gradually decreased to attain the lowest value at the highest salinity level. Amino acid foliar application at 500, 1000, or 1500 mg L^{-1} offset the adverse effect of salinity to some extent. It decreased uptake of Na^+ and Cl^- and in the same time increased the amount of Mg, N, P, K^+, and Ca^{2+} in faba bean leaves compared with the respective salinity level.

Some other studies in Table 19.4 show the effect of organic fertilizer amendment and foliar spray on the nutrient uptake in crop plants under salinity.

Table 19.4 Effects of organic fertilizer amendment and foliar spray on nutrient uptake in crop plants under salinity stress (some selected data)

Nutrient	Salinity	Plant	Organic fertilizer	Foliar spray	Effect	References
Phosphorus	1000–5000 ppm	*Sweet fennel*	Poultry manure	–	Increased	Abou El-Magd et al. (2008)
	2000,4000,6000 mg/L	*Jatropha curcas*	Nile compost	–	Increased	Mazhar et al. (2011)
	3.46, 12.86 dS m^{-1}	*Cotton*	–	Humic acid	Increased	Rady et al. (2016)
	4.26 dS m^{-1}	*Maize*	Compost/vermicompost	–	Increased	Oo et al. (2013)
	150 mM	*Sunflower*	–	Potassium sulfate	No significant change	Akram et al. (2009)
	8.9 dS m^{-1}	*Tomato*	Organo-mineral fertilizer	–	No significant change	Rady (2012)
	3.13, 6.25 dS m^{-1}	*Faba bean*	–	Proline	Increased	Dawood et al. (2014)
	1000,2000,5000 ppm	*Wheat*	–	Micronutrient compound	Increased	El-Fouly et al. (2011)
	33, 66 and 99 mM	*Soybean*	–	Zinc	Increased	Weisanya et al. (2014)
Nitrogen	1000–5000 (ppm)	*Sweet fennel*	Poultry manure	–	Increased	Abou El-Magd et al. (2008)
	3.6 dS m^{-1}	*Ginger(rhizome)*	Vermicompost/biogas slurry	–	No significant change	Ahmad et al. (2009)
	2000,4000,6000 mg/L	*Jatropha curcas*	Nile compost	–	Increased	Mazhar et al. (2011)
	12 dS/m	*Mung bean*	–	Salicylic acid	Increased	Akhtar et al. (2013)
	3, 5 and 7 mmhos	*Lettuce*	–	Urea	Increased	Hasaneen et al. (2008)
	3.46, 12.86 dS m^{-1}	*Cotton*	–	Humic acid	Increased	Rady et al. (2016)
	4.26 dS m^{-1}	*Maize*	Compost/vermicompost	–	Increased	Oo et al. (2013)
	150 mM	*Sunflower*	–	Potassium sulfate	No significant change	Akram et al. (2009)
	8.9 dS m^{-1}	*Tomato*	Organo-mineral fertilizer	–	Increased	Rady (2012)

(continued)

Table 19.4 (continued)

Nutrient	Salinity	Plant	Organic fertilizer	Foliar spray	Effect	References
	3.13, 6.25 dS m^{-1}	*Faba bean*	–	Proline	Increased	Dawood et al. (2014)
	1000,2000,5000 ppm	*Wheat*	–	Micronutrient compound	Increased	El-Fouly et al. (2011)
Potassium	1000–5000 (ppm)	*Sweet fennel*	Poultry manure	–	Increased	Abou El-Magd et al. (2008)
	3.6 dS m^{-1}	*Ginger(rhizome)*	Vermicompost/biogas slurry	–	Increased	Ahmed et al. (2009)
	2000,4000,6000 mg/L	*Jatropha curcas*	Nile compost	–	Increased	Mazhar et al. (2011)
	3.46, 12.86 dS m^{-1}	*Cotton*	–	Humic acid	Increased	Rady et al. (2016)
	4.26 dS m^{-1}	*Maize*	Compost/vermicompost	–	Increased	Oo et al. (2013)
	150 mM	*Sunflower*	–	Potassium sulfate	Increased	Akram et al. (2009)
	6.1, 9.9 dS m^{-1}	*Sunflower and Safflower*	–	Potassium nitrate	Increased	Jabeen and Ahmad (2011a)
	8.9 dS m^{-1}	*Tomato*	Organo-mineral fertilizer	–	Increased	Rady (2012)
	3.13, 6.25 dS m^{-1}	*Faba bean*	–	Proline	Increased	Dawood et al. (2014)
	1000,2000,5000 ppm	*Wheat*	–	Micronutrient compound	Increased	El-Fouly et al. (2011)
	33, 66 and 99 mM	*Soybean*		Zinc	Increased	Weisanya et al. (2014)
Calcium	1000–5000 (ppm)	*Sweet fennel*	Poultry manure	–	Increased	Abou El-Magd et al. (2008)
	3.46, 12.86 dS m^{-1}	*Cotton*	–	Humic acid	Increased	Rady et al. (2016)
	4.26 dS m^{-1}	*Maize*	Compost/vermicompost	–	Increased	Oo et al. (2013)
	150 mM	*Sunflower*	–	Potassium sulfate	No significant change	Akram et al. (2009)
	8.9 dS m^{-1}	*Tomato*	Organo-mineral fertilizer	–	Increased	Rady (2012)

	3.13, 6.25 dS m^{-1}	*Faba bean*	–	Proline	Increased	Dawood et al. (2014)
	1000,2000,5000 ppm	*Wheat*	–	Micronutrient compound	Increased	El-Fouly et al. (2011)
	33, 66 and 99 mM	*Soybean*	–	Zinc	Increased	Weisanya et al. (2014)
Magnesium	3.13 and 6.25 dS m^{-1}	*Faba bean*	–	Amino acid	Increased	Sadak et al. (2015)
	4.26 dS m^{-1}	*Maize*	Compost/vermicompost	–	Increased	Oo et al. (2013)
	150 mM	*Sunflower*	–	Potassium sulfate	No significant change	Akram et al. (2009)
	1000,2000,5000 ppm	*Wheat*	–	Micronutrient compound	Increased	El-Fouly et al. (2011)
Sodium	1000–5000 (ppm)	*Sweet fennel*	Poultry manure	–	Decreased	Abou El-Magd et al. (2008)
	3.6 dS m^{-1}	*Ginger(rhizome)*	Vermicompost/biogas slurry	–	Decreased	Ahmad et al. (2009)
	3.46, 12.86 dS m^{-1}	*Cotton*	–	Humic acid	Decreased	Rady et al. (2016)
	4.26 dS m^{-1}	*Maize*	Compost/vermicompost	–	Decreased	Oo et al. (2013)
	150 mM	*Sunflower*	–	Potassium sulfate	No significant change	Akram et al. (2009)
	6.1, 9.9 dS m^{-1}	*Sunflower and safflower*	–	Potassium nitrate	Decreased	Jabeen and Ahmad (2011a)
	6.1, 9.9 dS m^{-1}	*Sunflower*	Vermicompost/biogas slurry	–	Decreased	Jabeen and Ahmad (2017)
	8.9 dS m^{-1}	*Tomato*	Organo-mineral fertilizer	–	Decreased	Rady (2012)
	3.13, 6.25 dS m^{-1}	*Faba bean*	–	Proline	Decreased	Dawood et al. (2014)
	33, 66 and 99 mM	*Soybean*	–	Zinc	Decreased	Weisanya et al. (2014)

(continued)

Table 19.4 (continued)

Nutrient	Salinity	Plant	Organic fertilizer	Foliar spray	Effect	References
Chloride	3.13 and 6.25 dS m^{-1}	*Faba bean*	–	Amino acid	Decreased	Sadak et al. (2015)
	150 mM	*Sunflower*	–	Potassium sulfate	No significant change	Akram et al. (2009)
	6.1, 9.9 dS m^{-1}	*Sunflower and safflower*	–	Potassium nitrate	Decreased	Jabeen and Ahmad (2011a)
	6.1, 9.9 dS m^{-1}	*Sunflower*	Vermicompost/biogas slurry	–	Decreased	Jabeen and Ahmad (2017)
	3.13, 6.25 dS m^{-1}	*Faba bean*	–	Proline	Decreased	Dawood et al. (2014)
Zinc	3.46, 12.86 dS m^{-1}	*Cotton*	–	Humic acid	Increased	Rady et al. (2016)
	1000,2000,5000 ppm	*Wheat*	–	Micronutrient compound	Increased	El-Fouly et al. (2011)
	33, 66 and 99 mM	*Soybean*	–	Zinc	Increased	Weisanya et al. (2014)
Fe	3.46, 12.86 dS m^{-1}	*Cotton*	–	Humic acid	Increased	Rady et al. (2016)
	1000,2000,5000 ppm	*Wheat*	–	Micronutrient compound	Increased	El-Fouly et al. (2011)
	33, 66 and 99 mM	*Soybean*		Zinc	Increased	Weisanya et al. (2014)

19.5.1.3 Water Relations

Leaf water potential, osmotic potential, and turgor potential are interrelated in plant cells and are markedly affected when plants are exposed to salt stress. Water relation parameters are negatively correlated with increasing salinity. Increasing salinity decrease water potential and osmotic potential and increase turgor pressure of plants (Khan 2001; Romero-Aranda et al. 2001). Leaf water and osmotic potential declines according to the osmotic potential of the rooting medium and the type of stress. If plant faces prolonged salt stress, it maintains its turgidity with the decline in osmotic potential (Parida and Das 2005). According to Tester and Davenport (2003), when plants are under stress, it changes internal water potential values to maintain turgor and water uptake for growth. Plants usually maintained their turgidity by osmotic adjustment under saline condition. The osmotica, i.e., essential elemental ions and organic solutes, build osmotic balance, control water influx, and enable turgor maintenance (Ahmad and Jabeen 2009).

Several research reports have provided evidence for a marked reduction in all water relation parameters under saline conditions (Khan et al. 2000; Gulzar et al. 2003; Siddiqi and Ashraf 2008; Mezni et al. 2010; Singh et al. 2010; Vysotskaya et al. 2010; Eisa et al. 2012; Shaheen et al. 2013; Álvarez and Sánchez-Blanco 2014).

Selected studies are there to focus on the effects of application of organic matter to salt-stressed soils to find evidences on the potential of organic fertilizer in improving water relation attributes of plants.

It appeared from Table 19.5 that plant under salinity stresses, i.e., ECe 5.9 and 9.8 dS/m, had lower water potential and osmotic potential as compared to that plant provided with vermicompost and biogas slurry as fertilizer under the same salinity treatment. Application of organic manures had shown improvement in leaf water potential and osmotic potential. They reduced the tendency of lowering these parameters and ameliorate the negative effects of salinity by enhancing the availability of some other essential cations and phytohormones (Ahmad and Jabeen 2009). Phytohormone, K, and Ca have been reported to play an important signaling role on the regulation of stomata (Sage and Reid 1994). Increase in K^+ and organic

Table 19.5 Effect of organic fertilizer on water relations of sunflower under different salinity levels

Sea salt concentration (g/L)	Organic manure	Water potential (MPa)	Osmotic potential (MPa)	Turgor potential (MPa)
0 (ECiw 0.5 dS/m, ECe1.5 dS/m)	C	−0.420 ± 0.049	−1.500 ± 0.017	1.080 ± 0.042
	VC+BGS	−0.120 ± 0.006	−0.900 ± 0.012	0.780 ± 0.006
3 (ECiw 4.8 dS/m, ECe 5.9 dS/m)	C	−1.060 ± 0.006	−2.510 ± 0.017	1.450 ± 0.012
	VC+BGS	−0.690 ± 0.017	−1.710 ± 0.012	1.020 ± 0.006
6 (ECiw 8.6 dS/m, ECe:9.8 dS/m)	C	−1.340 ± 0.006	−3.240 ± 0.012	1.900 ± 0.006
	VC+BGS	−0.970 ± 0.012	−2.200 ± 0.017	1.230 ± 0.006

Source: Adapted from Ahmad and Jabeen (2009)
The values are mean ± SE ($n = 3$)
BGS biogas slurry, *VC* vermicompost

ions increases osmotic activity and reduces water potential which results in an inward diffusion of water from the nearby cells to maintain the turgidity of cell. Rady et al. (2016) found increased relative water content (RWC) in beans plants treated by either 20 or 30 ton organo-mineral fertilizer (OMF) compost h^{-1}, as an alternative to 50% of the recommended NPK dose under salinity. The exogenous applications of gypsum and farmyard manure (FYM) in saline fields mitigate salinity effects on plant and positively affected water use efficiency of rice leaf (Cha-um and Kirdmanee 2011).

Foliar application of nutrients was found to be effective in alleviating the harmful effects of salinity on growth by improving plant water status. A negative relationship between plant water status and increasing salinity was observed in sunflower and safflower both. Foliar application of nutrient solution (i.e., H_3BO_3 at 5 ppm, Fe-EDTA at 5 ppm, and KNO_3 at 250 ppm) significantly reduced the decreasing tendency of water relation parameters under different levels of salinities (i.e., ECe 6.1 and 9.9 dS/m) (Table 19.6; Jabeen and Ahmed 2012a).

Foliar application of glycine betaine (GB) at 0, 50, and 100 mM enhanced leaf water potential of maize under salinity stress, whereas due to GB application, a slight decrease was observed in leaf osmotic potential in the salt-stressed plants which resulted in improved leaf turgor potential, thus contributing in osmoregulatory process. The significant improvement in plant water status might have contributed to better growth of maize under salt stress (Nawaz and Ashraf 2007). Foliar application of potassium sulfate (K_2SO_4) significantly improved growth of sunflower plants under salinity stress (150 mM) which was found to be linked with the improvement in stomatal conductance, water use efficiency, leaf turgor potential, and relative water content (Akram et al. 2009). Different levels of foliar-applied KH_2PO_4 proved to be effective in improving growth of sunflower under salt stress with the increased water use efficiency and relative water contents (Akram and Ashraf 2011). A major role of potassium (K) in plant cells is osmoregulation, which is marked by the status of osmotic potential (Ψs). Kaya et al. (2007) observed that foliar application of KNO_3 (5 mM) significantly improves relative water content (RWC) in melon (*Cucumis melo*) under salinity (150 mM NaCl). Improvement in all water relation parameters in plants pretreated with K under salt stress has also been reported by Kaddour et al. (2009) in *Arabidopsis,* Zheng et al. (2008) in winter wheat and Cha-um et al. (2010) in rice.

19.5.1.4 Photosynthetic Pigments and Proteins

The photosynthetic pigments of leaves generally decrease under salt stress. The oldest leaves start to develop chlorosis and fall with prolonged period of salt stress (Parida and Das 2005). But there are some evidences which proved that chlorophyll content increases under salinity conditions (Wang and Nil 2000). Soluble protein contents of leaves usually decrease in response to salinity (Parida et al. 2002; Parida and Das 2005). But different views are there regarding increasing or decreasing proteins in plants under saline conditions. Amini and Ehsanpour (2005) reported

Table 19.6 Effect of foliar application of nutrients and their mixture on water relations of sunflower and safflower plants under different salinity levels

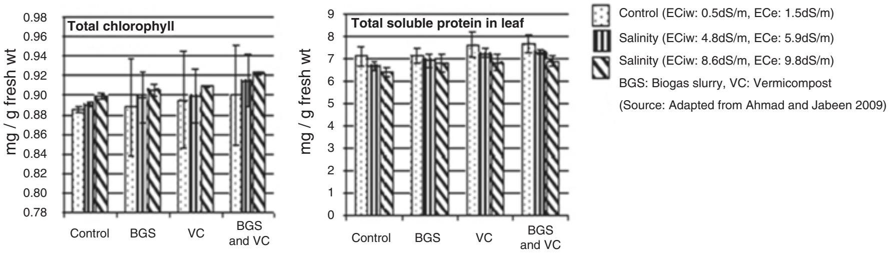
		Sunflower				Safflower			
Sea salt concentration (g/L)	Foliar spray treatment	Water potential (MPa)	Osmotic potential (MPa)	Turgor potential (MPa)	RLWC (%)	Water potential (MPa)	Osmotic potential (MPa)	Turgor potential (MPa)	RLWC (%)
0 (ECiw:0.5 dS/m, ECe:1.8 dS/m)	Control	−0.46 ± 0.05	−1.51 ± 0.11	1.05 ± 0.10	90 ± 2.2	−0.50 ± 0.07	−1.58 ± 0.06	1.08 ± 0.07	86 ± 1.2
	KNO_3	−0.44 ± 0.04	−1.45 ± 0.05	1.01 ± 0.08	90 ± 2.3	−0.47 ± 0.04	−1.56 ± 0.03	1.09 ± 0.05	88 ± 1.1
	H_3BO_3	−0.41 ± 0.03	−1.36 ± 0.05	0.95 ± 0.06	93 ± 2.6	−0.44 ± 0.05	−1.51 ± 0.04	1.07 ± 0.03	90 ± 0.6
	Fe-EDTA	−0.42 ± 0.06	−1.36 ± 0.11	0.94 ± 0.05	92 ± 1.2	−0.45 ± 0.06	−1.52 ± 0.05	1.07 ± 0.04	89 ± 0.6
	KNO_3+H_3BO_3+ Fe-EDTA	−0.44 ± 0.05	−1.46 ± 0.06	1.02 ± 0.05	91 ± 1.2	−0.47 ± 0.05	−1.56 ± 0.07	1.09 ± 0.06	88 ± 0.3
3 (ECiw:4.8 dS/m, ECe:6.1 dS/m)	Control	−1.06 ± 0.05	−2.52 ± 0.12	1.46 ± 0.12	79 ± 1.1	−1.12 ± 0.05	−3.08 ± 0.21	1.96 ± 0.17	74 ± 1.2
	KNO_3	−1.01 ± 0.05	−2.30 ± 0.15	1.29 ± 0.17	81 ± 0.6	−1.05 ± 0.02	−2.99 ± 0.15	1.94 ± 0.05	76 ± 1.2
	H_3BO_3	−0.97 ± 0.05	−2.15 ± 0.12	1.18 ± 0.13	83 ± 1.2	−1.01 ± 0.01	−2.90 ± 0.17	1.89 ± 0.07	78 ± 1.7
	Fe-EDTA	−0.99 ± 0.04	−2.16 ± 0.23	1.17 ± 0.17	83 ± 0.3	−1.01 ± 0.04	−2.91 ± 0.13	1.90 ± 0.05	77 ± 0.6
	KNO_3+H_3BO_3+ Fe-EDTA	−1.01 ± 0.05	−2.30 ± 0.20	1.29 ± 0.12	81 ± 1.2	−1.06 ± 0.02	−3.00 ± 0.13	1.94 ± 0.07	76 ± 2.3
6 (ECiw:8.6 dS/m, ECe:9.9 dS/m)	Control	−1.61 ± 0.12	−3.57 ± 0.21	1.96 ± 0.20	67 ± 1.7	−1.50 ± 0.07	−3.75 ± 0.21	2.25 ± 0.16	61 ± 1.2
	KNO_3	−1.56 ± 0.17	−3.52 ± 0.19	1.96 ± 0.16	69 ± 1.2	−1.46 ± 0.03	−3.69 ± 0.19	2.23 ± 0.20	63 ± 1.7
	H_3BO_3	−1.54 ± 0.15	−3.49 ± 0.17	1.95 ± 0.15	71 ± 0.6	−1.41 ± 0.05	−3.63 ± 0.17	2.22 ± 0.24	66 ± 1.6
	Fe-EDTA	−1.54 ± 0.23	−3.49 ± 0.24	1.95 ± 0.16	70 ± 0.6	−1.41 ± 0.05	−3.64 ± 0.19	2.23 ± 0.20	64 ± 2.3
	KNO_3+H_3BO_3+ Fe-EDTA	−1.56 ± 0.15	−3.53 ± 0.12	1.97 ± 0.13	69 ± 1.7	−1.46 ± 0.03	−3.69 ± 0.20	2.23 ± 0.20	63 ± 1.7

Source: Adapted from Jabeen and Ahmad (2012a)
The values are mean ± SE ($n = 3$)

increased soluble proteins in leaves and stem of tomato growing under saline conditions. It has been reported in some cases that soluble protein may increase at low salinity but decrease at high salinity (Agastian et al. 2000).

There are evidences which shows organic fertilizer offset the salinity effect and increase significantly the amount of photosynthetic pigments and total soluble proteins. Application of Nile compost at 0, 100, and 200 g/pot under three levels of salinity of diluted seawater (i.e., 2000, 4000, and 6000 mgL^{-1}) increased significantly chlorophyll a and b and carotenoid content percentage of *Jatropha curcas* (Mazhar et al. 2011). Total chlorophyll and total carotenoid of *Phaseolus vulgaris* were observed to be reduced in saline soil, treated with 10 ton ha^{-1} organo-mineral fertilizer (OMF) compost as an alternative to 50% of the recommended dose of NPK (Rady et al. 2016). Abdel-Ati and Eisa (2015) indicated highest significant observations in total chlorophyll content of barley (*Hordeum vulgare* L.) obtained from applying the rice straw compost (RS-compost) followed by rice straw with olive mill wastewater compost (RS-OMW compost) and 30 m^3 fed^{-1} of animal dung with no significant differences in between and the animal dung conventional dose, respectively, under salinity. The amount of chlorophyll a in rice leaf was decreased by 5.4%, 19.6%, and 26.4% at 0.3%, 1.0%, and 2.0% salinity levels, respectively.

Same trend was followed by chlorophyll *b*, total chlorophyll and total carotenoids. The chlorophyll *a* content was stabilized in the saline soil (1–2% salt levels) treated by organic manure at 12.5 kg m^{-2}. Total chlorophyll was better maintained in rice plants grown with organic manure treatment in 2% salt levels than in the control. The reduction in photosynthetic pigments in rice plants was directly related with the induction of salt contamination (Cha-um and Kirdmanee 2011). Total chlorophyll content in flag leaf of rice grown under salinity (ECe 12.5 dS m^{-1}) was decreased with the increase in sodium ions. Chlorophyll b and total chlorophyll content were maintained better in soil treated with both gypsum ($CaSO_4.2H_2O$) and farmyard manure (FYM) at 62.5 g m^{-2} and/or 500 g m^{-2}, respectively, than in the control. Similar results were observed in the treatment solely of gypsum or FYM, except for chlorophyll a and total carotenoids (Cha-um et al. 2011). Ahmad and Jabeen (2009) observed that total chlorophyll of sunflower did not increase significantly by the application of organic manure under non-saline condition, but these values considerably increased in salinity, whereas application of organic manure shows slight increase in protein under non-saline and insignificant difference under saline condition (Fig. 19.2). Ahmad et al. (2009) observed that the amount of chlorophyll in ginger leaves was significantly increased only in plants under non-saline condition provided by vermicompost as fertilizer and its concentration was reduced under saline water irrigation and remained more or less equal even in those plants provided with organic fertilizers (i.e., vermicompost and biogas slurry), whereas soluble proteins of leaves show some increase only under vermicompost amendment both under non-saline and saline conditions. The application of biogas slurry only and its mixture do not show any improvement in protein content. A significant decrease in total soluble protein content was recorded in sunflower with increased concentration of salts of rooting medium. Possibly the high salinity increases breakdown of protein due to proteolytic process.



(Source: Adapted from Ahmad and Jabeen 2009)

Fig. 19.2 Effect of organic fertilizer on total chlorophyll and total soluble protein of sunflower plant under different salinity level

Hussein et al. (2012) observed increased concentration of potassium monophosphate (KMP), i.e., 100 or 200 ppm in the foliar spray increased chlorophyll a, chlorophyll a + chlorophyll b, and chlorophyll a/chlorophyll b ratio in pepper (*Capsicum annuum* L.) plants irrigated with tap water (EC 0.47 dS/m) or increased saline irrigation water (4.69, 9.38 dS/m). The interactions between saline irrigation water and KMP levels in foliar spray were not significant on the concentrations of chlorophyll b and total carotenoids. Kaya et al. (2007) reported salinity (150 mM NaCl) decreased chlorophyll a and chlorophyll b contents in melon (*Cucumis melo*) and application of KNO_3 (5 mM) offset the negative effects of salt stress. Babar et al. (2014) reported salinity stress (100 mM NaCl) significantly reduced chlorophyll a and chlorophyll b of fenugreek. This decrease in chlorophyll might be due to the chlorophyll and other chloroplast pigments oxidation coupled with instability of the pigment protein complex under salt stress. Reduction in these chlorophyll contents was mitigated by the foliar application of salicylic acid at 100 mg L^{-1}. Azeem and Ahmad (2011) found foliar application of K along with Fe and B was found to be the most effective to increase photosynthetic rate by enhancing chlorophyll content in tomato (*Lycopersicon esculentum)* under different levels of salinity (ECiw 2.9 and 5.8 dS m^{-1}). Beside this they also reported increased protein content of leaves in plants being sprayed by Fe and mixture of K+Fe+B over their respective control. Chlorophyll content of strawberry leaves was reduced by 34% at 40 mM NaCl stress. Foliar application of KNO_3, $Mg(NO_3)_2$, and $Ca(NO_3)_2$ significantly improved leaf chlorophyll content. This might be attributed to the presence of magnesium ions in the center of chlorophyll molecules and the role of calcium to preserve the structural and functional integrity of plant membranes (Yildirim et al. 2009). Chlorophyll *a* and *b*, carotenoids, and total pigment contents of faba bean leaves reduced gradually at 3.13 and 6.25 dS m^{-1}. Foliar spray with amino acid at 500, 1000, or 1500 mg L^{-1} exerted stimulatory effects on photosynthetic pigments under both saline and non-saline (control) conditions. The increase in chlorophyll contents of sprayed plants might be attributed to the availability of amino acids as it helps to increase the chlorophyll level. Similarly protein content elevated with the elevation of amino acid up to 1500 mg L^{-1} at different salinity levels (Sadak et al. 2015). The highest observations were obtained in regard to the total chlorophyll (μmol m^{-2}) of barley plant under salinity from zinc sulfate foliar application with

30 ppm followed by 20 ppm and then 10 ppm and then the control treatment, respectively (Abdel-Ati and Eisa 2015). Chlorophyll a, chlorophyll b, total chlorophyll, and total carotenoid concentrations in salt-stressed (200 mM NaCl) leaves of Pathumthani 1 (PT1) rice seedlings were at 167.02, 53.72, 220.74, and 82.20 μg g^{-1} FW in 11.8 mM KNO3-treated seedlings which were greater than those without KNO_3 by 2.49, 2.49, 2.49, and 2.54 times, respectively (Cha-um et al. 2010). Foliar application of gibberellic acid at 100 mg L^1 solution was found to be the most effective for resisting the severe salinity effects on the chlorophyll contents of maize plant leaves followed by the applications at the same rates of silicon and then the salicylic acid (Rashad and Hussien 2014). Foliarly supplied KNO_3 (50 and 100 mM) significantly showed better tolerance of coriander plants toward salinity (40 and 80 mM NaCl), and positive significant effects were reported on plant protein and chlorophyll contents by Elhindi et al. (2016).

Zhang et al. (2013) found inhibition in protein synthesis of tomato plants by saline-alkaline stress. Exogenous spermidine (Spd) treatment facilitated to produce new proteins and/or accelerate the process of some original protein synthesis to adjust osmotic potential of cells to maintain turgor potential and alleviate damages that result from salt stress. Total soluble proteins (TSP) in different mung bean varieties decreased with increasing salinity, and maximum reduction in TSP was observed at 12 dS m^{-1}. Foliar application of salicylic acid (SA) at 100 mg L^{-1} was effective in alleviating the adverse effect of salinity and significantly increased the TSP (Akhtar et al. 2013). Bybordi and Mamedov (2010) reported that protein content was increased in canola plants being sprayed by micronutrients, i.e., iron + Zn. Rizk and Abdo (2001) found increased crude protein contents in mung bean with the foliar application of boron. Jabeen and Ahmed (2011b) reported increased protein content in sunflower with the foliar application of boron and manganese irrespective to the plant growth under non-saline or saline conditions. Data in Table 19.7 shows an increased total chlorophyll and total protein content in sunflower plant with the foliar spray of micronutrients (i.e., B and Mn) irrespective to their growth under saline or non-saline conditions (Jabeen 2010). Application of N as a liquid spray on wheat at late growth stage resulted in higher grain protein as compared to its broadcast as dry granular fertilizer (Bly and Woodard 2003; Fageria et al. 2009).

19.5.1.5 Nitrogen Metabolism

Nitrogen is an important element for the plant metabolism and to increase its resistance to salinity. It is available to plants in the form of nitrates (NO_3^-) which is absorbed by roots, transported to the shoot, and accumulated in vacuole for the N assimilation. Nitrate uptake and transport appear sensitive to salinity; the repression of NO_3^- under salinity is found to be directly proportional to the increasing salt concentrations. The decrease in NO_3^- concentration under salinity might be due to the root disruption, total nitrogen and nitrate uptake inhibition (Parida and Das 2004), low loading of NO_3^- into root xylem (Abd El-Baki et al. 2000), and decreased NRA (Debouba et al. 2006). Under salinity chloride (Cl^-) may inhibit the uptake of

Table 19.7 Effect of foliar application of H_3BO_3, $MnCl_2$, and their mixture on chlorophyll contents and total soluble protein of sunflower plant under different salinity levels

Sea salt concentration (g/L)	Foliar application	Chlorophyll a	Chlorophyll b	Total chlorophyll	Total protein
		mg/g F.W	mg/g F.W	mg/g F.W	mg/g F.W
0 (ECiw:0.5 dS/m, ECe:1.8 dS/m)	Control	0.50 ± 0.01	0.80 ± 0.07	1.30 ± 0.06	25.8 ± 0.23
	H_3BO_3	0.58 ± 0.01	0.86 ± 0.02	1.44 ± 0.02	27.8 ± 0.29
	$MnCl_2$	0.62 ± 0.02	0.89 ± 0.03	1.51 ± 0.05	26.7 ± 0.29
	H_3BO_3+$MnCl_2$	0.63 ± 0.02	0.91 ± 0.13	1.54 ± 0.14	28.0 ± 0.29
4 (ECiw:6.1 dS/m, ECe:7.4 dS/m)	Control	0.51 ± 0.01	0.83 ± 0.01	1.34 ± 0.02	22.0 ± 0.29
	H_3BO_3	0.62 ± 0.02	0.88 ± 0.01	1.50 ± 0.02	24.7 ± 0.23
	$MnCl_2$	0.65 ± 0.02	0.93 ± 0.01	1.58 ± 0.04	23.6 ± 0.29
	H_3BO_3+$MnCl_2$	0.65 ± 0.02	0.96 ± 0.02	1.61 ± 0.02	24.8 ± 0.18
8 (ECiw:10.8 dS/m, ECe:12.2 dS/m)	Control	0.37 ± 0.06	0.48 ± 0.03	0.85 ± 0.09	15.8 ± 0.29
	H_3BO_3	0.44 ± 0.05	0.54 ± 0.05	0.98 ± 0.10	18.2 ± 0.35
	$MnCl_2$	0.47 ± 0.02	0.57 ± 0.03	1.04 ± 0.04	17.4 ± 0.29
	H_3BO_3+$MnCl_2$	0.48 ± 0.01	0.58 ± 0.03	1.06 ± 0.04	18.3 ± 0.35

Source: Adapted from PhD Thesis, Jabeen (2010)
The values are mean ± SE ($n = 3$)

nitrate by nitrate transporters, or salt ions may inactivate nitrate transporters which results in higher chloride accumulation in leaves (Jabeen and Ahmed 2011a). Reductions in nitrate uptake under salinity reduce NRA in leaves which might be due to enzyme degradation/inactivation and the reduction in gene expression and NR protein synthesis (Debouba et al. 2007). Low levels of NO_3^- and glutamine in leaves may results the reduction in NR mRNA levels (Ferrario et al. 1998). Reduction in NO_3^- and NRA under salinity was also reported in leaves of olive trees by Tabatabaei (2006), in tomato by Debouba et al. (2007), in algarrobo by Meloni et al. (2004), and in soybean by Moussa (2004).

The nutrient supply methods can be modified to offset the harmful effect of salinity. Application of NO_3^- through foliage has been proved to improve the tolerance of plant to salinity by raising the nitrate content in plants (Ebert et al. 2002; Kaya and Higgs 2003). Albassam (2001) found in pearl millet under salt stress that addition of 10 mM nitrate in irrigation solution decreased Cl^- and activated NRA by increasing NO_3 uptake.

The highest values of NO_3, NRA, and NiR were recorded by Jabeen and Ahmad (2017) in sunflower plants grown in saline and non-saline soil amended with vermicompost as compared to those grown in soil amended with biogas slurry. At ECe 6.1 and 9.9 dS/m, an increase of 19.1% and 17.98%, respectively, was recorded in NRA in plants treated with vermicompost. This might be attributed to the supply of nutrients specially N through organic manure to the plant. An elevation of NRA resulted in an increase in nitrate reduction, which led to the total N assimilation (Ruiz et al. 2000). The increase in glutamine synthetase (GS) and glutamate synthase (GOGAT) activity of sunflower leaves irrespective of non-saline and saline water irrigation has also been reported with the amendment of vermicompost and biogas slurry by Jabeen and Ahmad (2017) (Table 19.8).

Table 19.8 The amount of nitrate and nitrogen assimilating enzymes

Sea salt concentration (g/L)	Organic manure	Nitrate µmole (g. f.w)$^{-1}$	NR (µmol NO_2 h^{-1} g fwt^{-1})	NIR (µmol NO_2 h^{-1} g fwt^{-1})	Glutamine synthetase (GS) (µmolγGH h^{-1} fwt^{-1})	NADH-glutamate synthase (µmol NADHox h^{-1} g fwt^{-1})	NADH-glutamate dehydrogenase (µmol NADHox h^{-1} g fwt^{-1})
0 (ECiw:0.5 dS/m, ECe:1.8 dS/m)	C	25.2 ± 1.5	9.3 ± 1.0	326.3 ± 8.2	285.6 ± 2.8	2.093 ± 0.4	13.75 ± 1.25
	VC	28.8 ± 1.0	12 ± 1.1	333.5 ± 4.5	292.3 ± 2.89	2.31 ± 0.35	13.88 ± 1.02
	BGS	27.3 ± 1.2	10.6 ± 1.3	329.9 ± 6.3	289.5 ± 4.6	2.22 ± 0.45	13.51 ± 1.66
3 (ECiw:4.8 dS/m, ECe:6.1 dS/m)	C	23.7 ± 1.2	8.68 ± 0.88	328.5 ± 4.8	278 ± 4.4	2.052 ± 0.42	14.99 ± 1.89
	VC	26.7 ± 1.6	10.73 ± 1.56	333.2 ± 5.9	290 ± 5.4	2.2 ± 0.56	15.00 ± 1.11
	BGS	25.0 ± 2.0	9.20 ± 1.12	330 ± 6.6	282.5 ± 5.4	2.15 ± 0.55	14.92 ± 1.3
6 (ECiw:8.6 dS/m, ECe:9.9 dS/m)	C	18.5 ± 0.8	7.3 ± 0.8	258 ± 2.9	190 ± 2.2	1.14 ± 0.02	17.32 ± 1.1
	VC	21.8 ± 0.58	8.9 ± 0.28	277.6 ± 3.33	196.4 ± 2.58	1.25 ± 0.01	17.52 ± 1.23
	BGS	19.73 ± 0.55	6.5 ± 0.35	263.9 ± 3.36	192.7 ± 1.89	1.19 ± 0.01	17.77 ± 1.31

Source: Adapted from Jabeen and Ahmad (2017)

The values are mean ± SE ($n = 3$)

NR nitrate reductase, *NIR* nitrite reductase, *GS* glutamine synthetase, NADH-glutamate synthase; NADH-glutamate dehydrogenase of sunflower plant irrigated with different concentrations of saline water with the amendments of organic manures in the soil

LSD: least significance difference is 0.05

Foliar supplied NO_3 through KNO_3 could decrease Cl^- concentration and offset its toxic effects by increasing the nitrate concentration. K^+ accumulation in leaves under salt stress maintain a high K/Na ratio which may help to regulate various enzymatic processes and protein synthesis.

In sunflower and safflower, Jabeen and Ahmad (2011a) found that application of foliar mineral KNO_3 significantly increased nitrate content and NR activity irrespective to their growth under non-saline (ECe 1.8 dS/m) or saline conditions (ECe 6.1 dS/m and 9.9 dS/m) (Table 19.9). Tabatabaei and Fakhrzad (2008) found in perennial ryegrass that 0–10 mM KNO_3 in the solution applied through soil or foliar increased NO_3^- concentration in leaves irrespective to plant growth under non-saline or saline conditions.

Application of 3–4% urea fertilizer through lettuce foliage under salinity significantly promoted activities of urease (UR), nitrate reductase (NR), glutamine synthetase (GS), and asparaginase (AS) (Hasaneen et al. 2008).

Foliar spray of 0.25 mM spermidine on tomato cultivars under saline-alkaline stress promotes NH_4^+ assimilation by coordinating and strengthening the synergistic action of NADH-GDH, GS/NADH-GOGAT, and transamination pathways. Later, NH_4^+, GDH, GS, GOGAT, GOT, and GPT are maintained in balanced state to mitigate harms caused by stress (Zhang et al. 2013). Foliar spray of salicylic acid at 100 mgL^{-1} under saline condition is found to be effective in the improvement of growth and yield of mung bean through improving the nitrogen metabolism by raising nitrogen uptake, NRA, NiRA, protein, and total amino acids (Akhtar et al. 2013). Foliar spray of KNO_3 with three microelement (Fe, Mn, Mo) mixture proved to be best spray medium to enhance the NRA in *Gossypium hirsutum* under different levels of salinity (Jabeen and Ahmad 2015).

19.5.1.6 Reproductive Yield

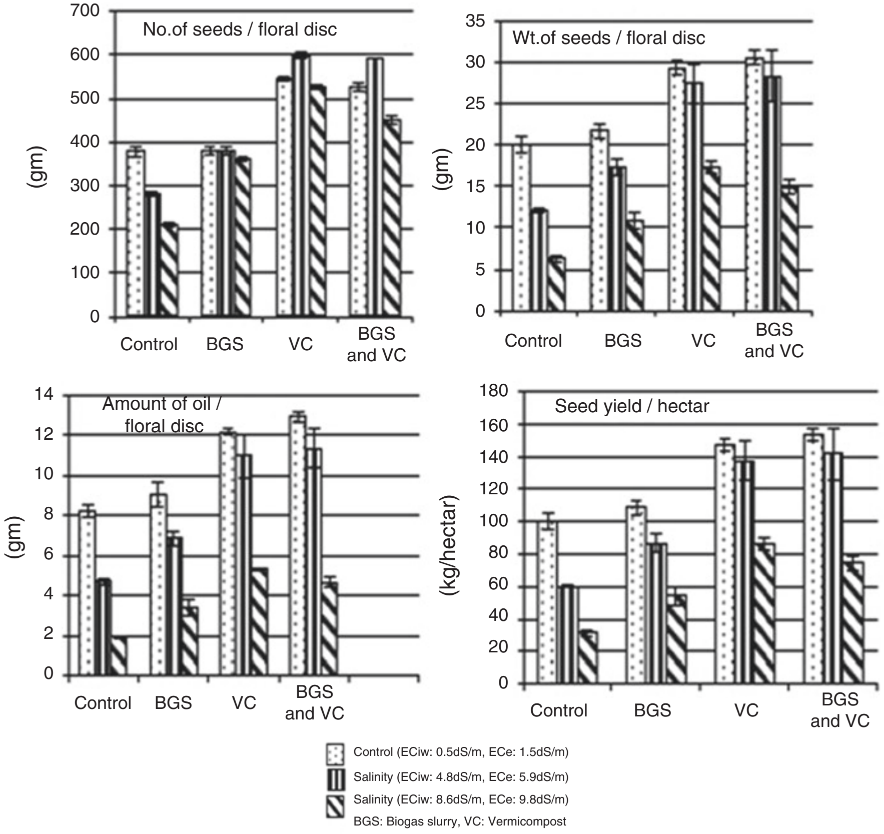
The soil or water salinity causes nutritional disorder related to mineral deficiencies which affect quality and quantity of marketable yield of fruits, roots, tubers, and leaves (Machado and Serralheiro 2017), e.g., irrigation with saline water causes blossom-end rot due to Ca^{2+} deficiency in some fruits and vegetables. Yield and quality of crop plants can also be affected by the timing of application of salt stress which could be important for improved irrigation and fertilization management strategies. Botía et al. (2005) observed that salt stress application at the time of fruiting till harvesting did not affect fruit quality and quantity of two melon cultivars.

A favorable pod and seed yield of common beans plant obtained with organo-mineral fertilizer (OMF) compost applied at 20 or 30 ton h^{-1} in the combination of 50% of the recommended dose of the NPK fertilizers under salinity. Application of 20 ton OMF compost ha^{-1} with 50% NPK has been found a better choice to achieve the greatest yields and to maintain soil fertility in the long run. It facilitates plants with potassium humate and sulfur to overcome the adverse effects of soil salinity as they work as additives for saline soils to improve crop productivity (Rady et al. 2016). Cha-um and Kirdmanee (2011) reported improvement in grain yield of rice

Table 19.9 Effect of foliar application of KNO_3 on amount of nitrate, nitrate reductase activity, and soluble proteins of sunflower and safflower plant under different salinity levels

		Sunflower			Safflower		
		Nitrate	Nitrate reductase activity	Soluble proteins	Nitrate	Nitrate reductase activity	Soluble proteins
Sea salt concentration (g/L)	Foliar spray treatment	μmole (g. f.w)$^{-1}$	μmole NO_2^- (g. f.w.h)$^{-1}$	mg/g f.wt	μmole (g. f.w)$^{-1}$	μmole NO_2^- (g.f.w.h)$^{-1}$	mg/g f.wt
0 (ECiw:0.5 dS/m, ECe:1.8 dS/m)	Control	25.6 ± 2.5	9.42 ± 0.98	25.8 ± 1.19	24.0 ± 1.74	5.45 ± 0.8	11.70 ± 1.12
	KNO_3	29.4 ± 2.2	10.95 ± 1.3	29.2 ± 1.12	27.1 ± 1.48	6.30 ± 0.72	13.26 ± 1.23
3 (ECiw:4.8 dS/m, ECe:6.1 dS/m)	Control	23.5 ± 1.8	8.71 ± 0.95	24.0 ± 1.2	19.8 ± 1.8	4.65 ± 0.2	10.00 ± 1.52
	KNO_3	27.5 ± 1.99	10.29 ± 0.89	27.9 ± 1.5	23.0 ± 1.67	5.49 ± 0.2	11.90 ± 1.44
6 (ECiw:8.6 dS/m, ECe:9.9 dS/m)	Control	18.7 ± 1.0	7.10 ± 0.88	19.0 ± 0.8	13.5 ± 1.66	3.48 ± 0.33	7.33 ± 0.21
	KNO_3	22.5 ± 2.2	8.50 ± 0.58	23.3 ± 1.4	15.8 ± 1.1	4.10 ± 0.43	9.10 ± 0.22

Source: Adapted from Jabeen and Ahmad (2011a, b)
The values are mean ± SE (*n* = 3)



(Source: Adapted from Ahmad and Jabeen 2009)

Fig. 19.3 Effect of organic fertilizer on reproductive yield of sunflower plant under different salinity levels. (Source: Adapted from Ahmad and Jabeen 2009)

by the addition of organic matter, i.e., farmyard and green manure, in paddy fields which may act as salt ion-binding agents to detox the toxicity induced by salinity.

Similar findings have also been reported by others that remediation of saline paddy fields by OM improved rice productivity (Amanullah 2008; Ghafoor et al. 2008; Murtaza et al. 2009). Abdel-Ati and Eisa (2015) have found increased productivity (spike length, weight of 1000 grains, grain and straw yield) of barley with the application of organic fertilizer, i.e., rice straw compost (RS-compost) and olive mill wastewater compost (OMW compost), under saline conditions. Ahmad et al. (2009) observed that yield of ginger rhizome under saline water irrigation was reduced by 47.2% amendment of vermicompost increased it by 30.76% under non-saline condition and under saline water irrigation by 70.77% in comparison with its respective saline controls. The organic manures (i.e., vermicompost and biogas slurry) under salinity increased reproductive yield of sunflower. Amount of oil showed a marked increase from 4.71 to 11.33 g at ECe 5.9 dS/m and from 1.92 to 5.35 g at ECe 9.8 dS/m (Ahmad and Jabeen 2009; Fig. 19.3).

Zaki (2016) concluded that 70 kg N fed^{-1} and 10 ton compost fed^{-1} could make highest rice reproductive yield possible under high saline conditions. Humic acid application to saline soil (12.86 dS m^{-1}) significantly increased number of bolls by 25.4, seed yield 15.7%, lint yield 13.6%, and total yield 14.2% compared to plants grown in saline soil without humic acid application (Rady et al. 2016). Brunetti et al. (2007) found that wheat grain yield and the components of humic substance, such as humic acid and fulvic acid, are positively correlated. The application of gypsum ($CaSO_4$ $2H_2O$) at 62.5 g m^{-2} and/or farmyard manure at 500 g m^{-2} to the saline soil in paddy field significantly improved reproductive yield as compared to the control, i.e., without gypsum and farmyard manure (Cha-um et al. 2011). Abusuwar and El Zilal (2010) reported four times increased forage sorghum yield compared to the control with the application of farmyard manure in a saline-sodic soil.

In order to observe the effects of foliar application on yield under salinity stress, extensive work has done in different crops. Sadak et al. (2015) revealed a significant increased reproductive yield of bean plant with the foliar application of amino acid at 1500 mg L^{-1} under tap water or different saline irrigation water. Fruit yield of salt-stressed *Lagenaria siceraria* was improved by foliar application of KNO_3 at 2.47 mM (Ahmad and Jabeen 2005). A significant increase was noticed by Azeem and Ahmad (2011) in yield (number, weight, and circumference of ripen fruits) of tomato crop plant by foliar spray of K, Fe, and their mixture (K+Fe+B) under saline conditions, i.e., ECe 4.31 dS/m and ECe 6.5 dS/m. Use of Mn foliar application had the highest positive effect on yield components and grain yield of sunflower crop plant under water stress condition (Babaeian et al. 2011). Foliar application of potassium sulfate (K_2SO_4) at 1.5% K+0.62% S and 1% K+0.41% S, respectively, improved growth and achene yield of sunflower plant under salinity (i.e., 0 and 150 mM). Improved growth and yield of sunflower plants due to K_2SO_4 application could be to the enhanced photosynthetic activity and other water relation parameters (Akram et al. 2009). Similarly Akram and Ashraf (2011) found varying levels of foliar-applied KH_2PO_4 (5+4, 10+8, 15+12, and 20+16 mg g^{-1} K + P, pH 6.5) effectively improved yield of sunflower at 150 mM NaCl stress. It has also been reported by Akram et al. (2007) that foliar spray of potassium hydroxide (KOH) at 0, 0.5, 1.0, 1.5, and 2.0% increased yield of sunflower under nonstress and salt-stressed conditions by improving K^+/Na^+ ratio. Foliar application of 200 ppm potassium monophosphate (KMP) increased the pepper plant fruit yield grown with different saline irrigation water, i.e., 3000 and 6000 ppm (Hussein et al. 2012). Abdel-Ati and Eisa (2015) indicated that foliar application of zinc sulfate ($ZnSO_4$) into barley plants led to increase the plant reproductive yield as a result of enhancing the plant metabolism and growth. The highest results were obtained from zinc sulfate foliar application with 30 ppm followed by 20 ppm and then 10 ppm and then the control treatment, respectively. Jabeen et al. (2013) found a significant reduction in oil content of seeds and oil yield per sunflower plant with the increasing concentration of sea salt solutions. Spray with H_3BO_3 and $MnCl_2$ exerted a significant effect and increased seed oil content and oil yield per plant irrespective to their growth under different saline irrigation water (ECiw 6.1 and 10.8 dS/m). Mn is found to have more stimulatory effect on oil yield than boron (Table 19.10).

Table 19.10 Effect of foliar application of H_3BO_3 and $MnCl_2$ on reproductive yield of sunflower plant under different salinity levels

Sea salt concentration (g/L)	Foliar application	No. of seeds/ plant	Weight of seeds/plant (g)	Amount of oil in seeds/plant (g)	Oil content in seeds (%)
0 (ECiw:0.5 dS/m, ECe:1.8 dS/m)	Control	$384.0^{ab}\pm6.55$	$19.97^{ab}\pm0.80$	$8.90^{b}\pm0.41$	$44.90^{ab}\pm0.42$
	H_3BO_3	$512.0^{a}\pm9.81$ (+25%)	$29.69^{a}\pm0.76$ (+32.7%)	$13.34^{a}\pm0.34$ (+ 33.3%)	$48.50^{a}\pm0.28$ (+7.4%)
	$MnCl_2$	$528.0^{a}\pm10.50$ (+27.3%)	$30.62^{a}\pm0.75$ (+34.8%)	$13.77^{a}\pm0.47$ (+ 35.4%)	$48.80^{a}\pm0.46$ (+8.0%)
0.4 (ECiw:6.1 dS/m, ECe:7.4 dS/m)	Control	$332.0^{bc}\pm6.93$ (−13.5%)	$14.94^{ab}\pm0.62$ (−25.2%)	$7.70^{b}\pm0.29$ (−13.5%)	$38.90^{b}\pm0.40$ (−13.4%)
	H_3BO_3	$458.0^{b}\pm2.73$ (+27.5%)	$23.91^{b}\pm0.25$ (+37.5%)	$12.00^{ab}\pm0.14$ (+ 35.8%)	$43.50^{ab}\pm0.37$ (+10.6%)
	$MnCl_2$	$474.0^{ab}\pm8.66$ (+30.0%)	$24.74^{b}\pm0.77$ (+39.6%)	$12.39^{ab}\pm0.31$ (+ 37.9%)	$43.90^{ab}\pm0.25$ (+11.4%)
0.8 (ECiw:10.8 dS/m, ECe:12.2 dS/m)	Control	$242.0^{c}\pm8.87$ (−37%)	$7.86^{c}\pm0.97$ (−60.6%)	$5.58^{c}\pm0.35$ (−37.3%)	$28.00^{c}\pm0.38$ (−37.6%)
	H_3BO_3	$338.0^{bc}\pm6.87$ (+28.4%)	$13.11^{abc}\pm0.43$ (+40%)	$9.00^{bc}\pm0.18$ (+ 38.0%)	$33.00^{bc}\pm0.86$ (+15.2%)
	$MnCl_2$	$348.0^{bc}\pm4.07$ (+30.5%)	$13.50^{abc}\pm0.21$ (+41.8%)	$9.25^{bc}\pm0.06$ (+ 39.7%)	$33.40^{bc}\pm0.27$ (+16.2%)

Source: Adapted from Jabeen et al. (2013)

Figures in parenthesis indicate % promotion (+) and reduction (−) over control. (Reduction percentage due to different salinities of irrigation water in non-spray plants has been calculated in comparison with non-saline control, whereas promotion due to foliar spray has been calculated over their respective non-spray control undergoing various saline irrigation.) The values are mean ± SE ($n = 3$)

19.6 Conclusion

The plant responses and tolerance mechanisms to different abiotic stresses need further critical physiological and molecular studies. It is a need of a time and a challenging task for plant scientists to explore the easiest and effective ways to overcome the adverse effects of stresses. This chapter provides a brief overview of the recent knowledge regarding the provision of essential mineral to plant to maximize the crop yield under stress due to salinization conditions through different approaches, i.e., organic fertilization amendments in soils and foliar application of nutrients. The overview, focusing on recently published data, aimed to investigate the potential and effects of these approaches to restore soil and crop quality.

Selected studies have identified organic materials (e.g., farmyard manures, different types of composts, different agro-industrial by-products, slurry, etc.) as effective tools to improve different soil properties in salt-affected soils to make it fertile for increasing food production. In our recent agricultural system, we have to feed the soil with the plants. Feeding the soil only compensate for the elements that have been spoiled and are not available for the plant. It has been revealed that organic fertilization being a good source of nutrients is highly productive and sustainable, but there is a need to consider this option as a solution to resolve the highlighted issues raised due to salinization of land.

It has also been proved that foliar application of nutrients could maximize crop yields under stress. The potential of foliar application of nutrients has gained significant attention in recent times, and many plant studies have revealed its protective roles in stress tolerance. However the rate of nutrient penetration through the barriers, i.e., cuticle or the stomata of leaf, into the cells depends on the concentration and the physical and chemical properties of the sprayed ion. Plant age and timings of nutrient application should also be considered to enhance its efficiency. The published literature indicates that foliar fertilization in crops increased yield, but the yield response of crops to foliar fertilization of macro- and micronutrients is highly variable. Foliar fertilization should be implemented at that time when soil-applied nutrients are ineffective due to their immobilization.

However, findings from experimental field research studies confirm that appropriate application of nutrients through organic fertilizer in soil or through foliar spray can be an effective protectant for crop plants for combating salinity stress.

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Chapter 20
Aspects of Co-tolerance Towards Salt and Heavy Metal Stresses in Halophytic Plant Species

Alina Wiszniewska, Iwona Kamińska, Aleksandra Koźmińska, and Ewa Hanus-Fajerska

Abstract In this chapter we were focused on physiological adaptations related to co-tolerance of plants towards salt and trace metal or metalloid stresses. Numerous halophytes, well adapted to grow in saline conditions, are concurrently able to accumulate elevated quantity of some trace elements, such as zinc, nickel, cadmium, lead or arsenic. The mechanisms underlying the tolerance to both, heavy metal or metalloid and salt toxicity level, include mainly typical defence reactions to oxidative stress and rearrangements in mineral status of particular organs which alleviate the negative consequences of stress in co-tolerant taxa. We discuss this unique feature on several examples of halophyte species tolerant to excessive amounts of trace elements, showing mechanisms which determine plant defence under intensive abiotic stress of that kind. We also discuss on the role of mineral status and ion homeostasis in developing the tolerant response on the phenotype level and compare mineral homeostasis between metal-tolerant halophytic and glycophytic species, sensitive to increased salinity.

Keywords Combined stress · Salinity · Cross tolerance · Plant stress · Nutrient homeostasis

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20.1 Introduction

Soil salinity and toxic compounds accumulating in the top layer of the earth surface, along with drought and elevated temperature stress, are the major problems which occur in agricultural areas all around the globe. They give rise to enormous yield losses or totally discriminate some areas or/and plant species from cultivation (Wang et al. 2003; Salewski et al. 2010; Duarte and Fonesca 2014; Feng et al. 2015; Marasco et al. 2013; Sandoval et al. 2016; Wang et al. 2016). However, plants resistant to particular stress often exhibit increased tolerance to other kinds of stresses. Recent studies revealed that halophytes, adapted to increased soil salinity, have at the same time higher level of ability than non-halophytic species to cope with drought and metallic stress (Bankaji et al. 2014; Moray et al. 2016; Shen et al. 2017). Heavy metal (HM) pollution became a serious threat to both natural and agricultural ecosystems, and now it is a real challenge to reduce the risk of human exposure to the most toxic HMs, such as mercury (Hg), cadmium (Cd) and lead (Pb) (Li et al. 2014, Lutts et al. 2016). Mechanisms determining plant tolerance to either salt stress or to HMs have been investigated intensively for last several years, but recently more and more attention is paid to co-tolerance of salt-resistant halophytes to trace elements. Halophytes became to be seen not only as the plants of elevated tolerance to salt stress but also as a potential solution for unwanted trace elements in agricultural soils (Nouri et al. 2017). Recent reports confirmed that halophytes developed co-tolerance to both heavy metal contamination and high salinity. Thus, halophytes are now being considered as model plants for understanding co-tolerance on salt and heavy metal stress in the plant kingdom because the same physiological processes are under impact of HMs or metalloids and salinity. Increased tolerance of halophytes to heavy metal ions allows them to grow in post-industrial areas (Toderich et al. 2010; Liu et al. 2017; Shen et al. 2017). Some hyperaccumulator plant species which are tolerant to salt stress developed adaptation to sustain high heavy metal concentration (Lutts and Lefevre 2015). This feature can be exploited for phytoremediation purposes of polluted sites, since numerous halophytes were found to either effectively accumulate heavy metals in the shoots or stabilize them in the rhizosphere (Lefevre et al. 2009; Clemente et al. 2012; Gonneau et al. 2014; Dixit et al. 2015, Nawaz et al. 2017). These properties give halophytes advantage over other species used to cope with problem of environmental pollution, such as numerous non-halophytic HM hyperaccumulators (Muszyńska and Hanus-Fajerska 2015; Wiszniewska et al. 2016, 2017a, b; Muszyńska et al. 2018). Thus currently, we can witness on a daily basis ground starting of the emerging field in plant science.

In this chapter we present recent findings concerning synergic tolerance of halophytes to high salinity and toxic metals and metalloids. We discuss the status of current research on halophytes grown in heavy metal-contaminated areas and specific features and adaptations of these plants that confer to their increased tolerance to environmental stressors. Besides, the mechanisms determining efficient stress response in halophytes subjected to heavy metals are reviewed here.

20.2 Studies on Halophyte Species Accumulating Environmental Pollutants

Valuable scientific field is to understand how particular plant species are adapted to grow in salt marshes, which are located on sediments deposited in estuaries, especially as such areas with its specific vegetation are deservedly considered natural sink for contaminants (Löser and Zehnsdorf 2002; Aksoy et al. 2005; Duarte et al. 2010; Cambrollé et al. 2011). It seems obvious that in connection with this important ecological function of these areas, there are especially sediments which act as main sink for trace elements, including numerous heavy metals (Table 20.1 and literature cited herein). Special concern is being given to the ballast elements, such as Hg, Cd or Pb (Fitzgerald et al. 2003; Windham et al. 2003; Weis and Weis 2004; Sousa et al. 2008; Caçador et al. 2009; Duarte et al. 2010; Anjum et al. 2012). That is why the effectiveness of halophyte and the so-called miohalophyte species to immobilize not only metals but also metalloids, especially arsenic (As) (Caetano et al. 2008; Paul and Shakaya 2013; Fernández et al. 2016; Ellili et al. 2017), is extensively studied, alongside numerous metallophytes belonging to non-halophytes (Dixit et al. 2015; Hanus-Fajerska and Koźmińska 2016; Ciarkowska et al. 2017; Wiszniewska et al. 2017a, b; Koźmińska et al. 2018). In salt marshes plants adapted to coastal areas may be frequently exposed to highly saline seawater inputs (González-Alcaraz et al. 2013). Rarely salt marshes occur inlands, where saline substrate is significantly diluted, especially during the long periods of rain. This results in higher seed germination rate of numerous species, also those less adopted to high salinity (Ingrouille and Eddie 2006; Ameixa et al. 2016). Consequently, in such areas environmental parameters and species composition are different from those formerly mentioned. Another kind of ecological niches is being created in arid areas and in highly evaporative climate, and as a result salt lakes or saline deserts represent extremely different habitats (Fernández et al. 2016). The next examples of halophytic maritime plant can grow on coastal cliffs, so in nature a broad gradient of tolerance both to concentration of chloride salt and other elements such as heavy metals can be encountered in particular species (Ingrouille and Eddie 2006). Similarly, it is vital that the existing knowledge should be advanced in the domain of the biogeochemistry at the rhizosphere of halophytes (Anjum et al. 2012; Ellili et al. 2017). Factors affecting the bioavailability of metallic or metalloid elements in the ionic form to the plant body include radiation influx, water or ground temperature, the humidity of substrate or sediment, its salinity, redox potential (Eh), particle size and organic matter content. Changes in temperature and of salinity alter metal speciation, and their uptake is above all important in the case of aquatic and wetland plants. Plant species growing in salty substrates are considered appropriate materials to be applied in an innovative approach, the so-called phytomanagement, with emerging fields of desalinization (Nedjimi 2014; Nouri et al. 2017) and phytoremediation of inorganic or organic pollutants from saline environments (Nazaré et al. 2011; Parraga-Aguado et al. 2014; Fernández et al. 2016; Ellili et al. 2017; Pérez-Sirvent et al. 2017). With the current pollution rate of multiple saline

Table 20.1 Important plant species studied in the area of salt marshes

Studied species in the area of salt marches and salty waters	The location of the study area	Examples of important study objectives	The results regarding interactions with heavy metals (HMs)	Additional remarks	References
Zostera capricorni, Zosteraceae	Pittwater, Australia	1. The effect of Cu, Zn, Cd and Pb on studied species 2. The study of seagrass recovery after (1 day) exposure to 0.1 or 1.0 mg L^{-1} of HM	After *Z. capricorni* exposure to a given HM solution for 10 h, Cu caused the greatest energetic cost (followed by Zn, then Cd and Pb)	The samples exposed to Zn, Cd and Pb recover, while those exposed to applied Cu levels might not recover to pre-exposure levels	Macinnis-ng and Ralph (2002)
Aster tripolium, Asteraceae; *Plantago maritima*, Plantaginaceae; *Phragmites australis*, *Agrostis stolonifera*, *Spartina* spp. Poaceae; *Schoenoplectus tabernaemontani* (syn. *Scirpus validus*), Cyperaceae	Four salt marshes in the Suir Estuary, Ireland	An comparative assessment of either Cu or Pb concentration in different plant organs and in the respective rhizosediments	In the case of studied dicotyledonous plant species, with the water salinity augmentation, it was ascertained the trend towards increased Pb translocation factor (TF)	In the population of *A. tripolium* partitioning of lead (Pb) in the plant body was definitely interconnected with higher or lower salinity level on particular plot in the studied salt marsh	Fitzgerald et al. (2003)
Phragmites australis, *Spartina alternifolia*, Poaceae	Salt marsh along the Jersey City Aqueduct in Lyndhurst, NJ, USA	The study of Cu, Zn, Cr, Pb and Hg, distribution in plant organs over one whole growing season in order to assess possibilities to reduce the water pollution	It has been proven that studied species possess different patterns of HM accumulation. Authors have suggested the use of *S. alternifolia* in order to decrease Hg and Cr export to the water	*P. australis* attained much higher biomass than *S. alternifolia* during the studied growth season	Windham et al. (2003)

Phragmites australis, Poaceae; *Ranunculus sphaerosphermus*, Ranunculaceae	Sultan Marsh on the Develi plain, Turkey	The evaluation of Cu, Zn, Cr, Cd and Pb sorption from polluted water and from rhizosediments	There was ascertained the relatively high Cd concentration in above ground organs of studied plant material	HM accumulation usually followed the typical sequence: root > stem > leaves	Aksoy et al. (2005)
Halimione portulacoides (syn. *Atriplex portulacoides*), Amaranthaceae	Tagus estuary salt marshes, Portugal	The assessment of the HM (Cu, Zn, Pb, Co, Ni and Cd) location both inside the organism and inside the cell	Most studied HM have been preferably accumulated in root with only limited transfer to shoots, whereas on the cell level the HM content was proved to be low in the protoplast	The majority of accumulated HM was bound to the cell wall, what was proved the main mechanism of plant detoxification from elevated levels of HM	Sousa et al. (2008)
Halimione portulacoides, *Sarcocornia fruticosa* *Sarcocornia perennis*, Amaranthaceae; *Spartina maritima*, Poaceae	Tagus estuary salt marsh and Guadiana salt marsh, Portugal	The verification of: (1) concentration of Fe, Mn, Zn, Cr, Ni, Cu, Co, As and Cd in above and below ground plant organs, (2) the enrichment factors (EFs) in two compared eustaries, (3) distribution of HM in plant organs over growing season	Only small amounts of studied trace elements were conducted upwards to the shoot and have been adsorbed on or accumulated in below ground organs. EFs in Tagus exceeded those from Guadiana reflecting more effective transfer from sediments to roots in the Tagus salt marsh. Pools of Cu and Co were higher in spring/summer.	*S. fruticosa* and *S. maritima* can be applied in order to accumulate Zn, Cu, As and Cd (and to a lesser extend also Cr and Ni) in root. The characteristics of *S. fruticosa* root system ensure stronger root-sediment interaction (more suitable for remediation purpose)	Caetano et al. (2008), Caçador et al. (2009), and Durate et al. (2010)

(continued)

Table 20.1 (continued)

Studied species in the area of salt marches and salty waters	The location of the study area	Examples of important study objectives	The results regarding interactions with heavy metals (HMs)	Additional remarks	References
Spartina maritima, *Spartina densiflora* Poaceae	Tinto-Odiel estuary salt marshes, Spain	The concentration of Co, Cr and Ni was assessed in plant organs as well as in rhizosediments	Both *S. maritima* and *S. densiflora* immobilized large amounts of Co from sediments and thus can be used to stabilize Co in the contaminated environment	Vegetation of salt plant marshes, and especially some vascular plant species, may be applied in remediation of HM polluted salty areas	Cambrollé et al. (2011)
Phragmites australis, Poaceae	The Ria de Aveiro coastal shallow lagoon, Portugal	(1) The determination of Hg concentration in the sediments and biomass	The highest levels of Hg concentration and translocation factor were recorded during autumn season	Since *P. australis* withstands the high Hg contamination, this particular species can be used during restoration scheme of the contaminated area of water	Anjum et al. (2012)
		(2) Comparison of bioaccumulation (BF) with translocation factor (TF)			
Sarcocornia fruticosa Amaranthaceae	Lo Poyo coastal salt marsh, Spain	Assessing the usefulness of both liming and phyto-management of wetland area heavily polluted with Zn, Pb, Cd and Cu	Liming decreased concentrations of soluble Zn, Cu and Pb but was ineffective in the case of Cd and Mn which increased, respectively	The study was scheduled as pot experiment with plant population from Lo Poyo costal salt marsh	González-Alcatraz et al. (2013)
Iris pseudacorus, Iridaceae; *Juncus effusus*, Cyperaceae *Phragmites australis*, Poaceae	Portman Bay, Spain	Experiment was done to assess usefulness of plant species under study to remediate Fe, Cu, Zn, Pb, Cd and As from coastal area with or without lime amendment	The highest Zn and Cd contents in roots of *J. effusus* and *P. australis* and of Cu in *P. australis* were revealed in plants growing in yellow fine texture sample	*I. pseudacorus*, *J. effusus* and *P. australis* can be used in remediation of HM polluted wetland area	Pérez-Sirvent et al. (2017)

environments, the situation in such different habitats has, unavoidably, become more and more complex. Thus, mechanisms responsible for parallel tolerance to these two different abiotic stressors are urgently needed to be elucidated in various plant materials. The efficacy criterions for applying plant material in the case of interconnected stresses are essential in restoration schemes. The extensive future studies in such an interdisciplinary domain are inevitable and should be rapidly undertaken.

Halophyte germinating, growing and completing life cycle under elevated salinity due to numerous adaptive traits may contribute to their better resistance to other kinds of stressors. Lutts and Lefevre (2015) reported that properties of halophytes involved in saline tolerance ensure heavy metal tolerance, since high heavy metal level causes an ionic toxicity, a secondary water stress and an oxidative stress. Furthermore, many of the salt-tolerant plants are quite well adapted to toxic metal-affected environments, and they are capable of remediating different HMs, grow and give yield (Anjum et al. 2014). Ability of accumulating enormous salt quantities by euhalophyte plant species has a great significance, particularly in semiarid and arid habitats, where the reduction of salt content in the rhizosphere is inefficient (sometimes impossible) due to insufficient precipitations and inappropriate watering systems (Shiyab et al. 2003). Numerous halophytes possess also features useful in desalination process, which are, apart from possibility to grow in highly salty stands, the effectiveness in biomass production, ability of sodium accumulation in above-ground organs and important opportunity of economic exploitation of biomass, for instance, as fodder, fuel, fibre, essential oil or oil seeds (Rabhi et al. 2010; Souza et al. 2012).

20.3 Specific Features of Halophytes in Relation to Mechanisms of Their Increased Resistance to Abiotic Stresses

Halophytes are roughly defined as plants with capability to complete life cycle in high salinity conditions (Stuart et al. 2012). These species can exist in an environment with a salinity concentration exceeding 200 mM of NaCl (~20 dS m^{-1}) (Flowers and Colmer 2008). According to Stuart et al. (2012), halophyte species constitute 1% of plants in the world. These specific taxa have developed a number of adaptations at the anatomical, morphological and physiological level that facilitate them to survive in salinity conditions (Table 20.1). The most specific mechanisms activated under saline condition include control of ion homeostasis, compartmentalization of toxic ions, maintenance of osmotic balance via synthesis and accumulation of osmolytes, succulence and salt inclusion or excretion (Munns and Tester 2008; Lokhande and Suprasanna 2012; Gupta and Huang 2014; Flowers and Colmer 2015).

20.3.1 Ion Homeostasis

Regarding the control of ion homeostasis, the pathways by which toxic ions enter an organism may involve ion channels, pinocytosis and ions transporters (Na^+ and Cl^-). Some halophytes have the ability to accumulate the Na^+ ions into the vacuoles in order to minimize its toxicity in the cytosol. Efficient sodium uptake into vacuoles or elimination outside the cell requires Na^+/H^+ antiporters, H^+-ATPases as well as H^+-PPIases to give the proton motive force. Another feature of halophytes is the presence of specific tonoplast antiporters which are absent from glycophytes. Moreover, in halophyte cells vacuoles are larger and have altered lipid composition to block leakage of sodium ions back to the cytoplasm (Glenn and Brown 1999; Gaxiola et al. 2007). Halophytic organisms have the capacity to reduce the ionic stress by reducing the amount of Na^+ that collects in the cytoplasm, particularly in cells of transpiring leaves (Carillo et al. 2011). These specific taxa have ability to lower uptake and concentration of toxic ions in the upper parts of the plant (Dajic 2006).

20.3.2 Salt Exclusion and Succulence

The possibility of salt exclusion depends on such factors as: uptake by root cells, preferential transport of K^+ instead of Na^+ into the xylem, the rate of salt discharging from the xylem in the upper parts of roots, stem and leaf veins correlated with phloem unloading (Hasanuzzaman et al. 2013). Moreover numerous halophytes, i.e. *Cressa*, *Frankenia*, *Spartina*, *Limonium*, *Plumbago* and *Tamarix*, developed multicellular excretory salt trichomes (Hasanuzzaman et al. 2013).Regarding succulence, halophytes have massive leaves and stems that are related with an increment in the volume of their mesophyll cells along with narrow intracellular spaces. They have numerous large mitochondria to fulfil energy requirements for salt compartmentalization and excretion (Lokhande and Suprasanna 2012).

20.3.3 Osmotic Adjustment

Among mechanisms of osmotic regulation are accumulation of salt, primarly NaCl, in the vacuole and accumulation of solutes, like proline, polyols, soluble sugars, glycine betaine (GB), alanine betaine, proline betaine, hydroxyproline betaine and pipecolate betaine in the cytoplasm (Rhodes and Hanson 1993). Apart from regulation of osmotic balance, these soluble compounds take part in detoxification of ROS, maintenance of membrane integrity and enzymatic balance and structural stabilization of proteins (Ashraf and Foolad 2007; Szabados and Savoure 2009). Accumulation of proline is one of the mechanism of osmoregulation that is used by halophytes like *Plantago crassifolia*, *Atriplex halimus* and *Phragmites australis*

(Vicente et al. 2004; Nedjimi and Daoud 2009; Pagter et al. 2009). Nevertheless, halophytes accumulate proline also under other abiotic stress conditions, like drought and heavy metal exposure (Slama et al. 2008). Glycine betaine (GB) is synthesized and accumulated in thylakoid membrane of chloroplasts (Robinson and Jones 1986). Enhanced synthesis and accumulation of GB protect cytoplasm from toxic ions, water loss and suboptimal temperatures, by stabilizing structures of macromolecules and protecting chloroplast and photosynthesis system II (PSII) from irreversible damage (Subbarao et al. 2001). It was proven that in reaction to salinity halophytes store higher GB amounts than glycophytes, reaching even 1.5–400 μmol g^{-1} DW in such species as *Halocnemum strobilaceum*, *Artemisia santonicum* and *Frankenia hirsuta* (Tipirdamaz et al. 2006; Lokhande and Suprasanna 2012). Accumulation of soluble sugars is another important feature of osmotic regulation in the halophytes (Yuanyuan et al. 2009). Briens and Larher (1982) reported that halophytic species such as *Plantago maritima*, *Juncus maritimus* and *Phragmites communis* accumulate sucrose, fructose and glucose at very high concentrations.

20.4 Mechanisms of Co-tolerance to Salt and Toxic Metal Stress

20.4.1 Physiological Effects of Salinity and Heavy Metals on Plant Cells

Physiology of plants tolerant to elevated salt level in soil was reviewed several times (Bartels and Sunkar 2005; Chinnusamy et al. 2005; Flowers and Colmer 2008; Munns and Tester 2008; Mane et al. 2011). Damaging effects of salt (mainly chlorides and sulphates of sodium, magnesium and calcium) on plant organs and cells are due to osmotic stress induced by low water potential of soil, ion toxicity by high accumulation of salt ions and ionic imbalance – lack of homeostasis in nutrient absorption. These factors cause disturbances at both cellular and organ level, such as mineral deficiencies in the cytoplasm, dehydration, decreased stomatal conductance, imbalanced concentrations of phytohormones, oxidative damage and suboptimal energetic requirements for ion transport and synthesis of 'compatible solutes' (Wang et al. 2003; Flowers and Colmer 2015).

Trace elements which occur in the soils, either essential or nonessential for the plant organism, may become toxic even in relatively small amounts above given threshold limit. Those substances trigger primary stress caused by ion toxicity and nutrient imbalance and secondary stress related with disturbances in water potential (water stress) and ROS generation (oxidative stress). Deficit or excess in level of important nutrients, enzymes inactivation, degradation of certain metabolites, membrane disruption, inhibition of electron transport in photosynthetic reactions and final loss of chloroplast functions, as well as DNA and protein injuries, are caused majorly by heavy metals (da Silva et al. 2010; Nagarani et al. 2012; Dixit et al. 2015). It leads to the disruption of important physiological processes. Decrease in transpiration is affected by limitations of water flow (Barcelo and Poschenrieder 1990) and water deficiency caused by disruption in leaf relative water content due to decrease of stomatal conductance (Ghelis et al. 2000; Vaillant et al. 2005). As a result, plant-water relationship is heavily disturbed mainly by inhibition in the root hairs emerging, decrease in membrane permeability and limited number of vascular bundles (Sghaier et al. 2015). Plants have developed different mechanisms to avoid HM toxicity: (a) inactivation of metals by chelation and sequestration; (b) osmotic and antioxidative protection of cell compartments and high-molecular-weight compounds (proteins, nucleic acids), osmoprotectants and antioxidative compounds synthesis via shikimate pathway and sulphur metabolism; and (c) morphological adaptations, excretion by trichomes and leaf succulence (Poschenrieder et al. 2006; Lutts and Lefevre 2015).

20.4.2 Co-tolerance of Halophytic Plants to Salinity and Toxic Trace Elements

The mechanisms responsible for co-tolerance can be found in the rhizosphere as well as in plant tissues. On a soil level, increased salinity affects mobility of the metal ions, especially Cu, Cd, Pb and Zn. To the metal mobility mechanisms are primarily classified competition with Ca and Mg ions for sorption sites on the solid phase (against Cd, Pb and Zn); complexation with chlorides and sulphates (and formation of $CuSO_4$) (Acosta et al. 2011). Different ions through their chemical properties affect heavy metal mobility on distinct levels: double-charge ions like Ca^{2+} or Mg^{2+} cause higher ion mobility than single-charge Na^+. On the other hand, heavier and larger ions hold mobilization. But the main effect of salinity is changing to higher pH the absorption edge of HMs, which decreases metal sorption to the soil particles and make them more available for the plants. According to Lutts and Lefevre (2015), halophytic plants have developed several types of adjustments to deal with heavy metals on a soil level:

(i) Impact on rhizospheric microorganisms (mostly bacteria). It can be driven through changes in pH or redox potential, which affects metal mobility. Supplementation of rhizosphere with different organic substances excluded from the roots as well as produced by bacteria can modify metal mobility (solubility, bioavailability). Metal ions can be fixed in complexes with either sulphide, oxalate or malonate (complexation) or with low-molecular-weight organic acids (e.g. citric acid) and high-molecular-weight substances (polysaccharides) as a chelating complexes.

(ii) Modification of the extracellular enzymatic activity (EEA). Xerohalophytes are expected to deal the best with heavy metal toxicity due to their adaptations to environments exhibiting low water availability. These plants developed efficient mechanisms of osmotic adjustment, which allow them to reduce water potential.

(iii) Formation of mycorrhiza, which helps to deal successfully with toxic ions.

Within the plant, tolerance and co-tolerance mechanisms can be related to transport and accumulation of salt and metal ions as well as osmotic and oxidative defence adjustments within the cells. Halophytes are dealing with high concentration of salt in the organs by osmotic adjustments and ion compartmentalization. According to Jones and Gorham (2002), monovalent ions become toxic at the concentrations needed for osmotic adjustments. It is fully accepted that compartmentalization is foremost mechanism involved in Na^+ and Cl^- detoxification. The cytoplasm is being secured against high concentration of those ions by locating them in the vacuoles. Experiments performed by Ratajczak et al. (1994) showed increased activity of tonoplast ATPase in the plants exposed to salinity stress. On the other hand, to balance the osmotic potential in the cytoplasm, 'compatible solutes' can be accumulated within the cells (mostly in the vacuoles) (Jones and Gorham 2002). Osmolytes function as chemical chaperones and scavengers of ROS, but mostly a wide range of water soluble molecules such as sugars and their derivatives (sugar alcohols), amino acids and their derivatives (methylated proline), betaines, tertiary sulphonium compounds and quaternary ammonium compounds are being synthesized to keep the osmotic balance (Flowers and Colmer 2008; Flowers and Colmer 2015). The same osmo-protecting compounds are also engaged in protection of cell's organelles in plants affected by heavy metals. Furthermore, amino acids, oxalates and cell wall polysaccharides can be involved in chelation and sequestration, similarly to processes that are abundant in the rhizosphere. Phytochelatins, active in the cytosol and sequestrating metal-binding complexes in the vacuoles, may be mentioned as the main group of chelators which could be rapidly synthesized in plants (Bankaji et al. 2016).

Salinity may reduce heavy metal absorption and through a dilution effect increase the rate of growth, plant tolerance to accumulated HMs (Lefevre et al. 2009; Xu et al. 2010; Han et al. 2012) and competition of ion uptake (Lopez-Chuken and Young 2005; Bankaji et al. 2014). It is interesting that roots exposed to salt and heavy metal stress accumulated less potassium and magnesium than those exposed to only one of those stresses. This effect can be considered as unfavourable, while the key advantage of halophytic plants in maintaining salt stress is ability to regulate Na^+ and Cl^- uptake simultaneously with efficient K^+ and Mg^{2+} cytosolic level for activation of essential enzyme activities (Flowers and Colmer 2015). Also, in contrast to single stress response, activity of antioxidant enzymes often decreases after combined treatment with heavy metal and salt (Bankaji et al. 2016). On the other hand, it has been ascertained that certain plants treated with arsenic were able to efficiently close their stomata in order to limit water loss, and as a major osmoprotectant they might accumulate betaines (Vromman et al. 2011; Lutts and Lefevre 2015). Another example of synergic behaviour is increased cadmium flow in xylem by Cl ions. Chloride promotes Cd releasing from Cd complexes and its fixation in Cd-Cl complexes, which are soluble and easily allocated within plant tissues or excreted by vesiculated hairs (Lefevre et al. 2009). Experiments on Zn with salt synergic effect on plant physiology show that Zn toxicity can be neutralized and growth can be improved when salt was added. According to Weis and Weis (2004), the higher electric conductivity would lead to metal uptake increase.

As mentioned above, plants possess anatomical adjustments to exclude Na^+ and Cl^- ions. Similar mechanism has been observed in the case of HMs. Sodium chloride treatment can increase the size and number of trichomes, which can excrete metal ions. Also, metal ions can be excluded by means of salt glands. Another anatomical adjustment of halophytes is leaf succulence. This feature is also in favour against possible cell toxic concentrations of HMs, because of dilution effect. Salinity, through increasing the leaves succulence, increases tolerance on high concentration of trace elements (Choi et al. 2004; Wang et al. 2012).

Salt stress as well as heavy metal stress affects photosynthesis, either by disruptions of photosynthetic apparatus or photosynthetic reactions. In glycophytes osmotic stress triggered by salinity causes dehydration and ABA elevation. As a consequence, stomatal conductance is affected, intracellular CO_2 level lowers, chloroplasts and chlorophyll level are reduced, D1 protein in PSII can be damaged, e-transport is altered, and RUBiSCO activity and ATP synthesis are declined. Moreover, ion toxicity causes thylakoid damage and grana stacking, and ionic imbalance leads to disorganization of PSII complex. Excess metals can cause similar disturbances, i.e. inhibition of chlorophyll synthesis, decreased levels of carotenoids in leaf tissues and low activity of PSII and Calvin cycle enzymes (Chaves et al. 2009). According to Redondo-Gomez et al. (2011) at midday there could be observed amplifying effect of Zn and elevated salt concentration on Fv/Fm values. Prasad and Strzałka (1999) reported that in high concentrations Zn interact with the donor side of PSII, inhibiting CO_2 fixation and the Hill reaction. Resulting absorption of excess energy by oxygen caused damage to the photosynthetic apparatus by producing ROS. However, sometimes the excessive excitation energy could be dissipated (Redondo-Gomez et al. 2011) mainly by electron flow from water in PSII to O_2 reduction in PSI, without a net change of O_2 concentration. On the other hand, Sghaier et al. (2015) did not observed any significant alterations in parameters related to PSII primary photochemistry under combined stress of salinity and arsenic contamination. Ability to dissipate excessive energy may be included to known mechanisms by which halophytes overcome the accumulation of excessive reducing power avoiding the destruction of the photosynthetic apparatus (Duarte and Fonesca 2014; Duarte et al. 2014). Furthermore, selenium application significantly reversed the negative effects of salinity on the photochemical efficiency of photosystem II (PSII) in glycophytes like tomato (Diao et al. 2014). The positive result of selenium is believed to be related to the regulation of antioxidant defence systems and photosynthesis (Jiang et al. 2017).

20.5 Mineral Homeostasis in Halophytes Grown Under Exposure to Trace Metals

The exposure to heavy metals usually affects concentration of mineral nutrients in plant organs. Changes in mineral homeostasis may be either directly related to displacement or substitution of nutrients with toxic ions, or indirectly, to disturbances in metabolic pathways caused by inactivation of enzymatic peptides and destruction of cell membranes (Rascio and Navari-Izzo 2011). Specific, organ- and tissue-dependent interactions between heavy metal and nutrient metal ions result in different responses to trace metals of the entire plant organism. Metal uptake and translocation within plants may also be manipulated externally by application of optimal doses of various nutrient elements (Siedlecka 1995). Such strategies have been recently developed, aiming at restriction of cadmium accumulation in crops (Sarwar et al. 2010; Su et al. 2014). Among numerous indicators of heavy metal resistance in plants is the ability to maintain adequate nutrient uptake, distribution and tissue concentration under exposure to metallic stress (Antosiewicz 1995; Sarwar et al. 2010; Gill and Tuteja 2011), and therefore heavy metal tolerance is often linked to plant ability to selectively absorb mineral elements from contaminated substrates (Kaldorf et al. 1999; Zaier et al. 2010).

Recently, due to their ability to cope with multiple stresses, halophytic species are considered valuable plant material suitable for phytoremediation of heavy metal-contaminated soils (Clemente et al. 2012; Lutts and Lefevre 2015). Numerous halophytic species have been reported to show increased tolerance to toxic metals, as well as capability to extract or stabilize metal ions, like Pb^{2+}, Cd^{2+}, Ni^{2+}, Cu^{2+}, As^{2+} and Zn^{2+} (Mateos-Naranjo et al. 2014; Rabier et al. 2014; Bankaji et al. 2015; Fourati et al. 2016; Vaněk et al. 2016; Guo et al. 2017; Nguyen et al. 2017; Santos et al. 2017; Shackira and Puthur 2017). Comparative studies examining heavy metal responses in halophytes and salt-sensitive glycophytes allowed distinguishing of stress tolerance mechanisms activated in halophytic species, i.e. increased antioxidant capacity, synthesis of metal chelates and maintenance of an adequate mineral nutrition level (Ghnaya et al. 2007; Zaier et al. 2010; Amari et al. 2016). Although the information on mineral status in halophytes exposed to metallic stress is limited, some interesting features of the mineral nutrition are pointed out below.

Majority of available studies reported on the differences in the concentration of macronutrients between halophytic and glycophytic species treated with toxic trace metals. Generally, under exposure to increasing heavy metal concentrations, halophytes are able to maintain higher level of macronutrients than glycophytic plants, even those metal-resistant. This reaction was observed in various halophyte species treated with Pb^{2+}, Cd^{2+}, as well as with multi-contaminated substrate (Ghnaya et al. 2007; Zaier et al. 2010; Bankaji et al. 2015; Guo et al. 2017; Santos et al. 2017). The most pronounced differences occur in the content of calcium, magnesium and potassium.

20.5.1 Calcium

Halophytes exposed to heavy metals are able to counteract calcium deficiencies more efficiently than glycophytes. In halophytic *Cakile maritima* only high doses of cadmium resulted in decreased concentration of Ca^{2+}, while in metal-tolerant glycophyte *Brassica juncea* the decrease was noted also in lower Cd^{2+} concentrations

(Taamalli et al. 2014). Also in Pb-treated shoots and roots of *Sesuvium portulacastrum* the level of Ca^{2+} remained unaffected, in contrast to *B. juncea*, where it was significantly reduced (Zaier et al. 2010). In turn, in *Iris lactea* and *Salicornia ramosissima*, greater accumulation of Ca^{2+} occurred with increasing concentrations of cadmium ions (Pérez-Romero et al. 2016; Guo et al. 2017). High level of calcium in plant tissues is related to tolerance response to heavy metal stress (Antosiewicz 1995). As signal molecules, Ca^{2+} ions regulate activity of antioxidant machinery and ROS generation, which is also crucial in stress tolerance (Maksymiec 2007). Since, according to Ghnaya et al. (2007), Ca deficiency considerably limits plant growth in stress conditions, the ability of halophytes to maintain adequate calcium level is crucial to exhibit growth tolerance under heavy metal exposure.

20.5.2 Magnesium

An increase in the content of Mg^{2+} in the shoots was reported in numerous halophytes exposed to heavy metals, for example, in *Suaeda fruticosa* (Bankaji et al. 2015) and *Iris lactea* (Guo et al. 2017), but also in metal-tolerant halophytes like *Zygophyllum fabago* (Lefevre et al. 2014), *Juncus acutus* (Mateos-Naranjo et al. 2014) and *Arthrocnemum macrostachyum* (Redondo-Gomez et al. 2010). In the case of roots, the level of magnesium usually remains unaffected (Redondo-Gomez et al. 2010; Guo et al. 2017). However, limited root uptake of Mg and Ca may be related to reduction in accumulation of toxic metals under saline conditions, what makes plant more tolerant to metallic stress (Mei et al. 2014). Magnesium is an important cofactor of enzymes and a component of photosynthetic apparatus. Its accumulation in the shoots can be therefore considered stress response directed at maintenance of high photosynthetic effectiveness under metallic stress (Guo et al. 2017). In fact, unaffected functioning of photosynthetic apparatus is observed in heavy metal-treated halophytes (Mateos-Naranjo et al. 2014; Taamalli et al. 2014).

20.5.3 Potassium

Halophytes, in contrast to glycophytes, accumulate higher level of potassium ions in leaf mesophyll, what contributes to their salinity tolerance (Percey et al. 2016). Similarly, under heavy metal exposure, such halophytes as *S. portulacastrum* (Zaier et al. 2010) and *C. maritima* (Taamalli et al. 2014) contained more K^+ than glycophyte *B. juncea*. Potassium status in the root of halophytes is more stable than in the shoots, and K^+ content in the roots remains unaffected even at very high concentrations of heavy metals. For example, exposition to 1000 mM $Pb(NO_3)_2$ resulted in significant K^+ deficiency in the roots of B. juncea, while in the roots of halophyte S. portulacastrum K^+ level was unaffected (Zaier et al. 2010). Potassium is a crucial element for water status regulation in plants, and changes in its concentrations determine opening and closure of stomata (Fageria 2015). Higher level of potassium in halophyte plants allows them to control water status more efficiently than it is in glycophytes. Moreover, in a situation of reduced K^+ uptake caused by high cadmium concentrations, halophytes are able to substitute K^+ ions with Na^+ in osmoregulation, what further increases their tolerance to water deficit (Ghnaya et al. 2007). These features confer to the higher resistance of halophytes to water stress induced by heavy metal exposure.

20.5.4 Other Nutrient Elements

Under intensive metallic stress, halophytes suffer from reduced concentrations of several nutrient elements, including iron, manganese and zinc (Taamalli et al. 2014; Guo et al. 2017). Interestingly, mineral disturbances are not manifested in the roots, suggesting that nutrient absorption and uptake by roots remains adequate (Guo et al. 2017). The level of several microelements, such as molybdenum, is considerably high in the roots of halophytes, most probably due to increased activity of enzymes (Pérez-Romero et al. 2016).

In halophytes exposed to toxic metals, status of sulphur nutrition was not widely investigated. However, when treated with heavy metals or salinity, halophytes use sulfur to produce sulpholipids, glutathione, phytochelatins and cysteine-rich amino acids (Hamed et al. 2005; Nguyen et al. 2017). As sulphur plays an important role in stress tolerance to both high salinity and heavy metal contamination (reviewed in Gill and Tuteja 2011; Nazar et al. 2011), research focusing on examination of sulphur status in the aspect of co-tolerance to these two stresses in halophytes would be of a great interest.

20.6 Conclusions

In conclusion, co-tolerance to salt and metallic stress is complex phenomenon and covers virtually every aspect of halophyte physiology. Salinity significantly modifies heavy metal uptake and deposition within plant organs and improves plant ability to survive in toxic substrate, for example, by reducing injuries caused by oxidative stress (Bankaji et al. 2016). The synergic effect between salinity and trace elements can be ascertained on multiple levels, starting in the rhizosphere, through organism, plant organs to cellular level. It is related to mobility and phytoavailability of ions, uptake processes, transportation, compartmentalization, photosynthesis and biosynthesis and antioxidant machinery. Heavy metal-tolerant halophytic plants could be valuable organisms for phytoremediation of polluted areas, and their properties give advantage over other species used to cope with environmental pollution problem. However, the information regarding the exact mechanisms and peculiarity of co-tolerance of trace elements on salt-stressed plants is still limited, and thus it is an emerging field of science to be further explored.

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Chapter 21
Role of Mineral Nutrients in Plant Growth Under Extreme Temperatures

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Abstract Food productivity is decreasing with the drastic increase in population, while it is expected that the global population will be nine to ten billion in 2050. Growth, production, and development on whole plant, cell, and subcellular levels are extremely affected by environmental factors particularly with the extreme temperature events (high- or low-temperature stress). Increase in the fluidity of lipid membrane, protein accumulation, and denaturation are the direct effects of high temperature on a plant. Membrane integrity loss, protein deprivation, protein synthesis inhabitation, and inactivation of mitochondrial and chloroplast enzymes are

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the indirect effects of high temperature. Similarly, the oval abortion, alteration of the pollen tube, reduction in fruit set, pollen sterility, and flower abscission are the consequences of low temperature at the time of product development, which in turn lowers the yield. The judicious nutrient management is essential for improving the plant nutrition status to mitigate the drastic effects of temperature stress as well as for sustainable plant yield under extreme temperature events, because nutrient deficiency results in growth and development problems in 60% cultivars worldwide. Additionally, effective nutrient management increases the temperature stress tolerance in plants. Therefore, the appropriate nutrient application rates and timings are imperative for alleviating the heat stress in plants and can serve as an effective and decent strategy. To minimize the contrasting effects of the environmental stresses, particularly heat stress, several examples of the supplemental applications of N, P, K, Ca, Mg, Se, and Zn are given in detail in this study, to observe how these nutrients reduce the effects of temperature stress in plants. This study concluded that judicious nutrient management minimizes the heat stress and increases the growth and yield of plants.

Keywords Environmental stress · Heat stress · Macronutrients · Micronutrients · Mechanisms

21.1 Introduction

Global temperature is gradually increasing due to industrialization, urbanization, and due to increasing greenhouse effect. The incidences of global climate change fortify the extra investment on ecosystem, life, and global economies than that of other sectors (Shakoor et al. 2011; Madzwamuze 2010; Hulme 2005), and affects the living standards of developing countries which already do not have access to modern technologies to overcome this problem (Madzwamuze 2010; OECD 2009).

The rise in temperature of an area results in climatic changes such as series of rainfall and rise in sea level, forced with a change in climate. The average rise of 2.8 °C in temperature increased the global temperature by 1.8–4 °C due to the deforestation, the concentration of carbon di oxide (CO_2) has raised from 280 to 380 ppm, and for this CO_2-enriched world and humans are responsible (Stern et al. 2006).

Climatic variables like temperature, sowing and harvesting dates, land, water, and rainfall pattern affect the productivity of crops and the agricultural commodities (Kaiser and Drennen 1993). High-temperature spells have been detected across Asia including Pakistan which is the second largest country in South Asia. This country has cold and dry regions having 49.6% population, and 22.8% area is at the risk of high temperature, frequent droughts and floods, glacier hideout, and rise in sea level. The effect of an increase in temperature even up to 1 °C is extremely disastrous for crop production in Pakistan due to agro-based nature of its economy and results in 6–9% decline in wheat production in the country. Agricultural productivity and growth decrease due to climate change-related threats, and the farmers of arid and hilly regions are harshly affected by these changes. Climate change poses serious threats to farmers of Asia living and growing crops in isolated and marginal areas such as mountains, dry lands and deserts areas which are deficient in natural resources. Temperature rise is expected in the arid areas of northern Pakistan and India as well as in western China (Shakoor et al. 2011).

The average temperature is rising, while rainfall is decreasing, and the agriculture sector in Pakistan will be more affected due to the climate change. A rise by 3 °C by 2040 and up to 5–6 °C is forecasted by the end of this century. These climatic changes have made agriculture sector economically vulnerable. Pakistan is at the 28th place among the countries that are going to be hurt hugely by climate change (MoE 2009).

Environmental factors are of different types and they affect the environment and living things in various means such as by affecting the productivity of plants during the flowering and fruiting phases. Water, light, temperature, nutrients, and atmosphere are most common environmental factors limiting crop production. Water is a crucial environmental factor which limits the endurance and growth of plants (Brown 1977). Less development and slow growth of roots and leaves were initially recorded if a plant was grown in a moist condition and then met moisture stress. Stomatal openings are less sensitive to water stress, while cell growth is more sensitive to water stress (Hsiao 1973).

Plants acquire CO_2 for photosynthesis and O_2 for respiration from the atmosphere. So if the atmosphere is polluted or affected by the pollutants, it may create a situation of an environmental factor for pants. Similarly, dry matter production is affected by the environmental factor due to their effects on carbon balance and exchange of CO_2 gas in the atmosphere (Larcher 1980). Production of dry matter is reduced by their relevant and unnecessary supply of nutrients. Different activities performed by the hormones in plants, carbon uptake, and transport of integrates are also affected by the environmental factors. Pollutants in the atmosphere are provided by the agricultural waste, transportation, industry, and chemicals, and these pollutants are also absorbed by the plants by water, soil, and air from the atmosphere (Larcher 1980). Hydrogen chloride, sulfur dioxide, peroxyacetyl nitrate, ozone, hydrocarbons, nitrogen, and dust are also pollutants in the atmosphere which are very hazardous to plants. Mixing of gases, physical damage to plant, and rise in evapotranspiration are the main influences of the wind which is also a component of the atmosphere affecting the plant productivity (Lauenroth et al. 1985).

Fire is one of the dangerous environmental factors which affect the plants directly by heat damage (Scifres 1980). Aerial stems of trees and shrubs have numerous growing points which are severely damaged by the heat of the fire (Young 1983). The plant growth generally depends upon the growth tips, so it's difficult for plants to survive after the heat of fire. Grazing has similar effects on the growth and shape of the plants like fire because a specific portion of the plants (leaves and tissue) is removed by the livestock, insects, or wildlife (Hyder 1972). Leaf sheaths and culms play an important role for the uptake of carbon during the specific time span of growth season (Caldwell et al. 1981). Nematodes are soil inhabiting and feed on plants (Smolik 1977). Reduced total forage of current-year crop is induced during the availability of sufficient moisture of soil, plant vigor reduction, and increase in leaf production which are the reasons of defoliation for regrowth in the flowering phase of current crop, and in the vegetative phase, defoliation has minimum effects on plant strength (Miller 1986; Eckert and Spencer 1987).

Reduced fodder production was reported by the nutrient insufficiencies in the soil (Vallentine 1980). In most of the places, major plant growth reduction was due to the nitrogen deficiency (Morrow et al. 1978; Fischer et al. 1987). Nitrogen fertilizer increases the fodder production of grasses through increasing the number and size of the roots, leaves, and stems as well as by increasing the seed production and forage quality by improving the water use efficiencies (Wight 1976; Power 1983; Rauzi and Fairbourn 1983). Like nitrogen, phosphorus either in high or low quantities in the soil can't support the fodder production in grasses or herbs (Vallentine 1980). Summer grasses do not respond favorably to nitrogen fertilizer, while the winter grasses respond favorably. Plant growth also depends upon the availability of nutrients for proper growth, height, shape, size, yield, and quality but if these nutrients are in excess or below the optimum requirement, the plant becomes under stress (Ata-Ul-Karim et al. 2016, 2017a, b). Shortage of nutrients is due to several factors, but nutrient deficiency is one of the environmental factors which affects the plants in all means (Vallentine 1980; Trappe 1981).

Due to climate change, plant scientists are facing a big problem of temperature stress worldwide; such stresses are actually bulging a potential impact on agriculture (Watanabe and Kume 2009; Shah et al. 2011). Every plant has specific optimum limits for temperature for survival, and such temperature stresses have severe effects on the metabolism and growth processes. Crop production is now restricted by the major abiotic stress of high temperature which is due to the changes in global climate (Hasanuzzaman et al. 2012). Increase in 4 °C temperature by the end of the twenty-fifth century is predicted by the models of climate and indicates more frequent heat waves in the future (Tebaldi et al. 2006; Hansen et al. 2015). The US Environmental Protection Agency (EPA) indicated that decades from 2000 to 2009 were the warmest ever and also directed the rise in the temperature during last 30 years (EPAA Student's Guide 2011).

Higher latitudes will be facing high change in temperature, while the temperature is increasing overall in the world, yet its effects on crops and plant vary according to seasons and regions. High-temperature stress is actually the increase in temperature for a period of time beyond a serious edge to cause a severe permanent damage to the development and growth of plants (Wahid 2007). Globally only 80,000 species of plants are edible to human from approximately 200,000 species of plants; only 20–25 species are providing 95% protein and calories to livestock and humans (Fu¨leky 2009). Likely 75% grain is produced globally by maize, rice, and wheat (Bansal et al. 2014; Lobell and Gourdji 2012). These edible or nonedible species include numerous biochemical reactions for growth and development; nonetheless, all these reactions are heat sensitive according to the types of plants and duration (Zróbek-sokolnik 2012; Mittler 2006). The decrease in temperature is also another environmental factor which affects the progression and enlargement of plants (Xin and Browse 2000; Sanghera et al. 2011). We review several researches in this chapter that discovered different responses of plants under the heat stress especially the nutrient uptake in heat stress.

21.2 Effects of Heat Stress on Plants

21.2.1 Physiological Effects of High Temperature

Change in the environmental temperature severely affects the physiological procedure of plant development, and high-temperature impact is determined by period, rate, and amount of temperature simultaneously (Wahid et al. 2007; Zinn et al. 2010). It's a very complex process for plants to manage with high temperature and is dogged by the environmental factors like the crop yield is affected by the soil and air temperature (Lobell and Gourdji 2012; Sharkey and Schrader 2006). Respiration increases with the increase in temperature up to a certain level and then starts to decline like photorespiration which is less delicate to temperature, but it also starts to decline when temperature rises beyond acritical level. Every 10 °C increase in temperature increases the enzymatic reactions by twofold, while the optimum temperature for enzymatic activity is 30–40 °C, and it will be deactivated or denatured if temperature is higher than 45 °C (Wahid et al. 2007; Bita and Gerats, 2013; Bokszczanin et al. 2013; Mathur et al. 2014). Plant development, crop duration, respiration, carbon assimilation, and all other growth processes were affected by the rise in temperature (Takeoka et al. 1991; Maestri et al. 2002; Stone 2001). Plant cell structure could be lastingly damaged by high temperature which leads to the plant death, and sexual reproduction is also negatively affected by the high temperature (Peet et al. 1997; Erickson and Markhart, 2002; Zinn et al. 2010; Zróbek-sokolnik 2012.).

21.2.2 Effects of Heat on Seed Germination and Emergence

Seedling vigor and germination are the most important traits to ensure the potential crop yield and good plant stands. Temperature is the elementary factor for the germination process as germination depends upon temperature in all crop species (Bac-Mole-naar et al. 2015; Giorno et al. 2013; Jagadish et al. 2014; Sakata and Higashitani 2008). The optimum temperature for wheat (*Triticum aestivum*), maize (*Zea mays*), watermelon (*Cucumis melo*), etc. is from 25 to 30 °C, while optimum temperature for lettuce (*Lactuca sativa*) and spinach (*Spinacia oleracea*) ranges from 15 to 20 °C. Similarly, the optimum temperatures for germination of seedlings in different crops vary from one crop to another, but optimum temperature for seed germination generally ranges between 15 and 30 °C (Saitoh 2008; Johkan et al. 2011). Another environmental factor which affects the germination of seeds is the soil temperature (Prasad et al. 2006a, b).

Three physiological processes during germination, dormancy loss rate in dry seeds, determination of germination rate in nondormant seeds, and corrosion rate of seeds by moisture, are influenced by temperature (Roberts 1988). Generally, the increase in temperature beyond the optimum temperature results in lower germination rates and even can cause cell death and embryo damage in various crop species (Prasad et al. 2006a, b; Essemine et al. 2010; Kumar et al. 2011). Shoots and roots of some species grown in hydroponic culture could bear the day/night temperature 35/25 °C (Piramila et al. 2012). High temperature also reduces the plant emergence and vigor index, but it is indispensable to relief the energy for germination, and summer- or warm-season crops require more temperature for growth and seed germination as compared to the winter crops (Piramila et al. 2012; Borthwick and Robins 1928; Stotzky and Cox 1962; Hall 2001).

21.2.3 *Effects of High Temperature on Crop Morphology and Growth*

Plant growth retardation is a common result of heat stress, and simultaneous occurrence of heat and drought events causes severe harmful effects on productivity and growth of plants. Plant height is reduced with the high temperature due to declined stem growth, while the weight and the size of leaf are reduced because of changes in the rate of cell elongation and detachment in the plant associated with high temperature (Prasad et al. 2006a, b). An experiment was performed to investigate the effect of heat on the growth of wheat, and results showed that the height of wheat plant was 66.4–97.3 cm under normal environment, while it ranged from 55.7 to 82.3 cm under heat stress treatment (Rahman 2004).

Growth is also influenced by the loss of water as a consequence of temperature rise, and high temperature reduces the size, length, and number of roots, relative growth rate, dry weight of shoots, and net assimilation rate in millet and maize (Al-Busaidi et al. 2012; Porter and Gawith 1999; Ashraf and Hafeez 2004). The effects of heat stress, such as reduction of plant water, increase in stomata and trachomatous densities, stomata closing and cell size, etc., have similar effects on internal morphology of plants as those under drought stress. Wahid (2007) and Zhang et al. (2009) performed experiments to observe the effects of heat on rice crop, and results showed that plants were highly affected by high temperature due to the weak structure and organs against the survival under high temperature. High night temperature effect was also observed in an experiment on wheat crop and detected that high temperature lessened the number of tillers (Johkan et al. 2011).

21.2.4 Effects of High Temperature on Photosynthesis

Photosynthesis and temperature have positive relationship up to an extent. Temperature plays a vital role for optimum photosynthesis, yet the rise in temperature above the optimum range results in destruction of enzymes associated with photosynthesis (Schuster and Monson 1990). The increase in photorespiration is higher than photosynthesis with increase in temperature. To investigate the effect of high temperature on photosynthesis in tobacco leaves, 38% active photosynthesis was left behind in 43 °C with the duration of 2 h which was back to 75% active after 1-day recovery (Tan et al. 2011). As compared to the optimum night temperature, photosynthetic rate and chlorophyll content were decreased to 22% and 8%, respectively, at high night temperature of 31.9 °C (Prasad et al. 2011).

Deactivation of rubisco by high temperature is the primary constraint of photosynthesis. Photosynthesis rates in *Eucalyptus haemastoma* and *Vitis vinifera* were controlled by stomatal conductance, and results showed that photosynthesis of these species was decreased due to the deterioration of stomatal conductance at high temperature of 40–45 °C (Haldimann and Feller 2004; Eamus et al. 2008; Greer and Weedon 2012). Chloroplast ultrastructure change and biosynthesis inhabitation occurred due to the reduction of photosynthetic pigments in high temperature (Tewari and Tripathy 1998; Reda and Mandoura 2011). It was also reported that chlorophyll ratio and contents were diminished by high temperature in *T. aestivum*, *Solanum* spp., *Festuca arundinacea*, etc. (Reda 2011; Aien et al. 2011). Several other climatic parameters were also involved in the effect of high temperature on crops. Photosynthetic rate of maize and pea leaves and photosynthetic response of potato were not affected by the high temperature (Wolf et al. 1990; Haldimann and Feller 2005; Suwa et al. 2010).

21.2.5 Effect of Heat Stress on Water Relation in Plant

Water position is considered as the most imperative variable in plants under the varying ambient temperature, and water relations in the plant were significantly influenced by drought and heat stress (Mazorra et al. 2002). Initially, the seedlings are affected by the rise in temperature due to tissue damage and raising the evaporative demand associated with increasing transpiration and transportation of water under high temperature which are the basic utensils for the subsistence of plants in heat stress.

Pinus ponderosa species was observed to check the water relation under high temperature, but a large number of seedling died when the temperature reached 63 °C. In high temperature, water plays an important role to cool down the plant through seedling stem water transport because sufficient energy is absorbed by quick water flow through the seedling stem and can reduce the temperature of the plant by 30 °C (Kolb and Robberecht 1996). Leaf turgor potential, leaf relative water content, soil water content, leaf water potential, osmotic adjustment, and leaf osmotic potential were observed by growing the *Hordeum vulgare* and *Triticum aestivum* in soil and chambers with well-watered and control conditions (water stress treatment) at day/night temperatures of 15/10, 25/20, 35/30, and 40/35 °C, and all water stress treatment plants were severely damaged at high temperature (Machado and Paulsen 2001; Banon et al. 2004). Water is necessary for life, and heat stress severely affects the water status in plants, so the reduction of water in plants due to heat could kill all the plants (Wahid and Close 2007).

21.2.6 Effects of Heat Stress on Dry Matter Partitioning

Mineral uptake and assimilation process become slower during the grain-filling stage under heat and water stress as well as under different temperatures that results in variation of dry matter partitioning in different crops (Gebbing et al. 1999). Leaf senescence doesn't occur under the high temperature because the sink activity lost when earlier panicle senescence happens and termination of grain filling occurs (Morita et al. 2004; Kim et al. 2011). Rice plants observed under the temperature command of 21.9 °C and 24.4 °C showed a cheap duration of leaf senescence and dry matter partitioning to panicle. Starch synthesis-related enzyme activity is damaged by several factors at high temperature due to lost sink activity. In rice grains, starch accumulation and grain sink strength are strongly associated with sucrose synthase movement (Mohapatta et al. 2009; Tang et al. 2009). Heat stress also showed the reduction in seed harvest index, total dry weight, and seed dry weight in the pot experiment with four genotypes of *Arachis hypogaea* (Morita et al. 2005; Craufurd et al. 2002). *Z. mays*, *Saccharum officinarum*, and *Pennisetum glaucum* were also observed under high temperature and showed a reduction in dry matter and growth rate (Wahid et al. 2007).

21.2.7 Effects of Heat Stress on Reproductive Development of Plant

Plant reproductive development is very sensitive to environmental factors especially to high temperature exposure because high temperature and fertility are inversely proportional to each other and some plant species even fail to set fruit under high temperature (Sato et al. 2006; Abiko et al. 2005; Prasad et al. 2006a, b; Oshino et al. 2007; Jagadish et al. 2009; Zinn et al. 2010; Peet et al. 1998; Mckee and Richards 1998; Abdul-baki and Stommel 1995). Fruit set reduction was also observed in another experiment on peach and bean due to the low pollen viability in high temperature (Peet et al. 1997; Erickson and Markhart, 2002; Barnaba's et al. 2008; Gross and Kigel 1994, Kozai et al. 2004, Sato et al. 2000). Abnormalities in anther and pollen development also occurred in *Phaseolus vulgaris* in heat stress, while low pod setting was observed in soybean because flower development and differentiation occur under high temperature (Porch and Jahn 2001; Kitano et al. 2006). For proper growth and development of reproductive parts in plants, day and night temperature is very important; however, some species like rice is sensitive to night temperature due to spikelet fertility because the rise in night temperature is inversely proportional to numbers of fertile spikelet (Zakaria et al. 2002; Peng et al. 2004). In another experiment shorter time of ripening and reduced number of flowers and fruits at 30/25 °C were also witnessed in two varieties of strawberries (Ledisma et al. 2008).

21.2.8 Effects of High Temperature on Crop Yield

Crop yield depends upon the crop vigor, crop growth, photosynthesis, and DM partitioning of the plant, but these all are negatively affected by the high temperature. Therefore, crop yield is ultimately affected by the high temperature through affecting both sink and source for assimilates. High temperature reduced the endosperm cell area by which the length and width of cereal grains were decreased (Ulukan 2008; Levy and Veilleux 2007; Luo 2011; Saha et al. 2010; Morita et al. 2005). In another study, high temperature effects were observed on the B-73 inbred line of maize, and data showed that the kernel growth rate was increased with high temperature but dry matter accumulation duration was reduced. During the endosperm cell division, the development of endosperm stops due to the high temperature which reduces the leaf area, shoot biomass, grain yield, and sugar content of kernel (Zakaria et al. 2002; Shah and Paulsen 2003; Monjardino et al. 2005). *Sorghum bicolor* were grown under normal (32/22 °C) and high temperature (40/30 °C) to observe the heat effect. Sorghum yield was decreased to 99% due to high temperature, and leaf dry weight, plant height, total dry weight, and seed weight were also reduced by 14%, 22%, 36%, and 53%, respectively, in comparison with optimum temperature (Djanaguiraman et al. 2010).

Wheat crop is very sensitive to high temperature as compared to the other crops. In an experiment collected data showed that wheat crop is severely damaged by the high temperature and 50% reduction was observed in the numbers of grain per spike, 39% in grain yield and 24% in harvest index of wheat under high temperature (Mohammed and Tarpley 2010). High temperature effects on crop yields were observed in many other trials like the yields of *Cicer arietinum*, *Sorghum bicolor*, *Triticum aestivum*, *Oryza sativa*, *and Capsicum annum* which were reduced to 48%, 10–99%, 46%, 90%, and 62%, respectively, due to high temperature (Mendham and Salsbury 1995; Gan et al. 2004; Lin et al. 2010; Saha et al. 2010; Mohammed and Tarpley 2010). Due to the increase in temperature, the reproductive stage of plants becomes defenseless in crops like rapeseed, sunflower, soybean, tomato, etc. because the flower abortion and lower fertility could occur under high temperature (Barnaba's et al. 2008; Hedhly et al. 2009; Zinn et al. 2010; Luo 2011; Jagadish et al. 2014; Maduraimuthu and Prasad 2014).

21.2.9 *Effects of Heat Stress on Nutrient Movements and Uptakes*

Cell membrane plays a major role in regulating inter- and intracellular movement of nutrients and water. The movement and transportation of nutrients and water inside or outside the cell become inhibited by high as well as by low temperature by damaging cell. Ion leakage is caused by the permeability of unwanted nutrients in membrane due to low-temperature stress. Low temperature can also rupture the cell wall and cell membrane which creates disturbing of cellular homeostasis. Low temperature creates the problem for the movement of water inside and outside the membrane of the cell by damaging the membrane (Salians 2002; Mahajan and Tuteja 2005). Fluid inside the cell has higher freezing point, so under the low temperature, ice formation starts in intercellular spaces when temperature drops below 0 °C. Therefore, severe dehydration could occur by freezing the water and solutes, while under higher temperature, the dehydration could occur due to overevaporation of water contents from plant (Thomashow 1999; Yadav 2010). In low temperature, difficulties occur in the closure of stomata and reduction of water and nutrient uptake which leads to the dehydration of cells, and low temperature also damages the endoplasmic reticulum and cortical cells like in the roots of cucumber. Thus it is very clear that the germination success or failure in the field depends upon the development of roots in cold temperature (Lee et al. 2002; Enns et al. 2006; Yadav 2010). Unprovoked water movement is also caused by the low temperature (Hurry et al. 1994).

Reliability of cell membrane and effect of silicon were observed in high temperature on stress tolerance of rice plants by measuring the electrolyte leakage from leaves. Si level has inverse relation with the polyethylene glycol solutions of 30% and 40% to cause the electrolyte leakage. In cell wall, levels of polysaccharides were 1.6-fold higher in plant leaves which were grown with 100 ppm SiO_2 than in the plants which were grown without Si. Similarly, the leaves of the plants grown in Si have low electrolyte leakage developed by the 42.5 °C of high temperature than in the leaves of plants grown without the Si. Consequently, it was concluded by this experiment that in the heat stress the weakening of function and structure of cell membrane was prevented by the Si (Nelson 1944). Crop growth and productivity are commonly devastated by the high temperature. The effect of selenium (Se) was checked in the experiment in which (75 mg/L) Se was sprayed at flowering stage and heat stress 40/30 °C was persuaded after spraying the plants of cucumber (*Cucumis sativus* L.) to observe the yield, physiochemical, and growth of plant for 75 days after sowing (Djanaguiraman et al. 2010; Abbas et al. 2015). Stomatal conductance, antioxidant enzymes, transpiration rate, yield, lipid peroxidation, chlorophyll content, and photosynthesis were affected by the heat stress, while the application of Se helps the plants by refining the development of plant components, antioxidants, enzymes, chlorophyll contents, Pn, etc. to moderate the heat stress (Balal et al. 2016).

Quality, growth, and yield of rice cultivars (IR-64 and Huanghuazhan) were observed in controlled growth chambers by adding phosphorus (P), different types of biochar, and mixture of these at control temperature (28 °C ± 2), high night temperature (32 °C ± 2), and high day temperature (35 °C ± 2) (Fahad et al. 2015; Hasanuzzaman et al. 2013; Liang et al. 2006). Growth and development of rice variety Huanghuazhan were better than other varieties in high temperature. Seven percent increase in growth and yield per plant was improved by the addition of the mixture of biochar and P. Intake of P and treated nutrient helps the plant to reduce the effects of heat stress by improving the water use efficiency and photosynthesis (Hasanuzzaman et al. 2013). External application of nitric oxide and sodium nitroprusside reduces the heat stress on chrysanthemum plant by slowing down the rate and pigment contents of photosynthesis in plant (Simontacchi et al. 2004). Moreover, it also facilitates the superoxide dismutase activities, catalase, peroxidase, and fluorescence by increasing the non-photochemical slaking (Yang et al. 2011). Sensitive Roma and tolerant Robin are the two cultivars of tomato which were observed to check their response under high temperature 40 °C by adding the small amount of ^{45}Ca in fruits (Starck and Witek-Czuprytika 1993). The major difference of the transportation of ^{45}Ca in fruit was observed at different temperatures with or without the application of plant growth regulators. Robin cuttings translocated higher part of ^{45}Ca in fruits under heat stress and then the cuttings of sensitive Roma while treated or not treated with the GA_3 + NOA (Brown and Ho 1993; Minamide and Ho 1993).

Heat and other environmental stresses are actually due to the global warming. Many experiments were performed on the nutrient uptake by plants under the heat stress, yet very limited data on protein nutrient uptake by the plant under the heat stress is available (Huang et al. 2012; Wahid et al. 2007; Hao et al. 2012). *Solanum lycopersicum* plants were grown at normal temperature (25 °C/20 °C) and then transferred to the high temperature (35 °C/30 °C or 42 °C/37 °C), while in the second experiment, day/night temperatures 28 °C/23 °C, 32 °C/27 °C, 36 °C/31 °C, and 40 °C/35ºC were applied to the *Solanum lycopersicum* plants for 15 days. In the first experiment, it was observed by enzyme-linked immunosorbent assay (ELIZA) and by using the protein antibodies that root/shoot mass ratio and N and C percentage were reduced in heat stress, while in another experiment, only extremely high temperature (40–42 °C) affects the roots, reduced the protein accumulation in roots, and reduced the concentration of protein (Mishra et al. 2012). So it was concluded that by distressing the root nutrient relationship, the heat stress could affect the quality and production of the crop (SOD enzymes provide strength to plant to mitigate the heat stress, but its activity and membrane integrity were affected by the Zn deficiency and heat stress (Foyer and Harbins 1994; Cakmak 2000; Rashid and Ryan 2004; Alloway 2008)). Three-day heat stress (40/20 °C) in the experiment of 10 days and 6-day heat stress (40/20 °C) on the experiment of 30 days were applied to wheat grown with short and satisfactory levels of Zn to investigate the effect of heat stress and Zn on two growth phases. Reduced kernel weight, grain yield, and growth rate occurred in plants containing low Zn under the heat stress in both sensitive and tolerant varieties. Heat stress with the low supply of Zn could reduce the chlorophyll content and disturbed the ultrastructure of chlorophyll of plants indicating that the less availability of Zn and high temperature could slow down the function of chloroplast and kernel growth (Alison and Glenn 2010). Sometimes two environmental factors like heat stress and nutrient deficiencies affect the crop instantaneously. Under heat stress, Mg-deficient plants showed serious visual leaf symptoms in wheat and maize. Root growth, shoot growth, and carbohydrate concentrations were also affected by the heat stress with joint effect of Mg deficiency (Fischer and Bremer 1993; Hermans et al. 2004; Cakmak and Yazici 2010; Gransee and Führs 2013). Nevertheless, antioxidative enzymes were increased when Mg-deficient stress combined with heat stress and up to 80% increase in the superoxide dismutase activities, 300% increase in ascorbate peroxidase, and 250% increase in glutathione reductase activities under the heat and Zn deficiency stress were observed by forming the ROS (Yamashita et al. 2008; Marutani et al. 2012; Suzuki et al. 2012).

In environmental stress, growth and response of plants at molecular, cellular, and tissue level are regulated by calcium (Ca) (Waraich et al. 2011). Prevention against the transpirational water loss and maintenance of leaf water potential are higher in plants which can tolerate the cold stress. In chilling tolerant plants, Ca is a basic requirement for stomatal closure even the Ca^{2+} mediate the stomatal closure induced by ABA (Wilkinson et al. 2001). Reduction in cold injury stress effects and recovery from injury are facilitated by the role of Ca by activating the ATPase (plasma membrane enzyme) (Palta 1990). Ca helps to pump back the nutrients in cold injury by releasing the ATPase. In cell structure, Ca also has a vital role in maintaining and controlling the metabolic activities of plants by calmodulin formation (Waraich et al. 2011).

Wheat plants treated with 5 mM $CaCl_2$ and those untreated faced the heat exposure of 43.5 °C, showed several changes in MDA, SOD, guaiacol peroxidase, and catalase, and it was concluded that Ca^{2+}-supplemented plants under the heat stress faced a short-term oxidative stress that is not associated with permanent damage (Bakardjieva et al. 2000; Jiang and Huang 2001; Kolupaev and Karpets 2003). Day/night temperature (42/30 °C), chlorophyll a, b, and photochemical efficiency were minimized in N-deficient plant by 13, 20, and 27%, respectively under the heat stress (Reynolds et al. 2000; Hassan 2006; Berry and Björkman 1980; Xu and Huang 2000; Zhao et al. 2008; Pelligrini et al. 2011; Murchie and Lawson 2013), while a significant rise of 32%, 60%, and 69% and by 25%, 88%, and 100% was observed in 5, 10, and 15 mM N-supplemented plants in all these parameters, respectively. Antagonistic effects of heat stress are reduced by the N fertilization (Hassan et al. 2015). To tolerate the heat stress, Ca is a gesturing molecule which helps the plant (Hu et al. 2012). Different biochemical and molecular parameters were observed on wheat crop under the heat stress (42 °C) for the period of 2 h with the exogenous application of Ca^{2+} at 10 mM. The negative relation was found between the exogenous application of Ca^{2+} and lipid peroxidation. In contrast, positive relationship with an antioxidant under the high temperature was observed (Sharma and Dubey 2005; Amirjani 2012; Benzie and Strain 1999). Ca^{2+} stimulates the heat tolerance and antioxidant capacity under high temperature.

The role of nitrogen is very dynamic in heat stress. Plant grows destructively, and nutrient uptake in plants is affected by the rising temperature and light intensity. For photosynthetic carbon breakdown and to consume the absorbed light energy, N plays a significant role (Kato et al. 2003; Huang et al. 2004). Photooxidative damage is caused by the non-utilized light energy in leaves which lacks N (Huang et al.

2004). Thylakoid membrane helps to avoid the photooxidative damage by its defensive machinery because photooxidative damage is tolerated by plants with a higher level of N than the plants with low N. Due to the fluctuations in xanthophyll cycle, pigments of spinach 64% and 36% absorbed light in N-deficient plant parts and N-sufficient plant parts, respectively (Verhoeven et al. 1997; Kato et al. 2003). With the combination of environmental stress, the N-deficient plants have a higher risk of photooxidative stress. Bean leaves with addition of nitrate have high conversion rate of violaxanthin into zeaxanthin in high light energy than plants with the application of ammonium. Consequently, antioxidant enzyme and lipid peroxidation level is higher in plants containing higher concentration of ammonium under the high light intensity (Bendixen et al. 2001; Zhu et al. 2000). Opposing effects of abiotic stresses like heat stress are alleviated by the N fertilizer, and N in many physiological processes is very responsive in the form of nitric oxide (Waraich et al. 2011; Zhao et al. 2007; Yang et al. 2006; Crawford and Guo 2005: Zhang et al. 2006).

Mineral nutrients play a fundamental role to enhance the plant resistance under high temperature and other environmental stresses (Marschner 1995). For many physiological processes like maintenance of turgidity, photosynthesis and enzyme activation, etc., potassium (K) is an essential nutrient. Its deficiency in plants could show a severe reduction in these processes (Marschner 1995; Mengel and Kirkby 2001). The membrane structure of the lipid membrane could be altered with the temperature stress. Due to the conversion of O_2 into ROS, the processes like stomatal conductance, CO_2 fixation, rubisco activity, and electron transport in photosynthesis are affected by low temperature (Huner et al. 1998; Foyer et al. 2002; Marschner 1995). Protection against oxidative stress damages is more in plants with high K than in plants containing a low supply of K. In carnation plants under the low temperature, high amount of K protects the plant from stem damage, and in potato plant, the adverse effects of low temperature such as low yield could be reduced by the K application (Grewal and Singh 1980; Kafkafi 1990).

In various biochemical and physiological processes, magnesium (Mg) is involved in facilitating the plant growth and development (Waraich et al. 2011). A small variation in the Mg level could affect the chloroplast enzymes, and photosynthesis of plant could also be affected by the excess or deficiency of Mg (Shaul 2002; Shabala and Hariadi 2005; Fischer 1997; Sun and Payn 1999; Ridolfi and Garrec 2000; Hermans and Verbruggen 2005). In different organelles, different metabolic pathways produce a by-product ROS under the temperature stress, which is a basic reason for the loss of production and could kill the plant cell by damaging the lipid, protein, DNA, and carbohydrates (Navrot et al. 2007; Tuteja 2007; Tuteja 2010; Khan and Singh 2008). Oxidative damage is also caused by the mineral deficiency. In beans, maize, pepper, and mulberry, concentration and activities of oxidative molecules and oxidative enzymes were increased by the Mg to avoid the oxidative damage (Halliwell 1987; Yu et al. 1999; Cakmak and Marschner 1992; Cakmak 1994; Tewari et al. 2004, 2006; Anza et al. 2005). For higher uptake of water and nutrients by the root, Mg increases the growth and surface area of roots to enhance the photosynthetic rate by maintaining the chloroplast structure under the heat stress (Waraich et al. 2011).

Micronutrients also play an imperative role for proper growth and development of plants under the heat stress. In cell division, cell elongation, membrane function, cell wall biosynthesis, uracil system, and N metabolism are the chemical and physiological processes in which B is directly or indirectly involved in plant growth (Marschner 1995). ROS are encouraged by the high-/low-temperature stress which could also stop the progression of the plant (Xu et al. 2008). ROS could be minimized by an increase in antioxidant activities with the application of B in plants, and seed formation and germination can also be enhanced by the improvement of sugar transportation plants with B. Cell damage reduction and increase in photosynthesis and crop yield were induced with the B application by minimizing the ROS production (Waraich et al. 2011).

In N metabolism, in photosynthesis, and in other metabolic processes of plants, manganese (Mn) is a compulsory micronutrient. An increase in physiological and morphological damages and reduction in uptake of nutrients in plants are caused by the heat stress. Mn increases the photosynthesis and N metabolism to reduce the adverse effects of heat stress on the plant. Leaf drop of premature plants and brown necrotic spots are also reduced by the application of Mn. In decarboxylation and oxidation reduction, many enzymes are activated with the involvement of Mn in plants grown under heat stress (Marschner 1995; Aktas et al. 2005; Turhan et al. 2006).

21.3 Effects of Nutrients on Heat Stress

In guaiacol peroxidase (GPXs), Se is present on an active site and executes as an antioxidant; therefore, it is one of the essential nutrients in animal and human nutrition (Djanaguiraman et al. 2010). Plant tolerance is increased by the Se under drought, heavy metal, and heat stress (Balal et al. 2016; Haghghi et al. 2014; Duran et al. 2016). It was observed in an experiment that heat resistance is enhanced in cucumber plants by the Se, which helps the plants for better growth and yield by maintaining the stomatal conductance; photosynthetic and transpiration rate was improved under high temperature with the foliar application of 8 μMSe (Balal et al. 2016). Antioxidant activities, chlorophyll contents, and osmotic adjustment capacity of wheat plants were increased and improved, while H_2O_2 contents, MDA, and electrolyte leakage were decreased with exogenous application of Se under heat stress (Iqbal et al. 2015). Similarly, in rice antioxidant activities were increased and oxidative stress was decreased by seed priming with (60 μM) Se, which in turn increased the heat stress tolerance in rice plant under high-temperature stress (Hussain et al. 2016). CAT, GR, MDHAR, SOD, and APX activities were increased in maize roots in hydroponic solution with Se application under heat stress. Oxidative stress was also reduced by the Se application under heat stress (Yildiztugay et al. 2017).

For metabolic processes in plants, different inorganic nutrients are required from which Ca is an important nutrient. Oxidative stress was reduced, and amino acid contents were increased in wheat crop grown under the heat stress with the application of Ca (Goswami et al. 2015). The increase in SOD, CAT, and POD activities in wheat crop followed similar patterns as that in maize crop under the heat stress by applying Ca (Kolupaev et al. 2005). Photosynthetic rate can also be increased in plants with an application on Ca under heat stress. Different concentrations of Mg (15, 20, and 540 μM) were applied to maize and wheat crops in hydroponic medium under heat stress and observed that biomass, growth, and heat tolerance were increased in plants under high concentration (540 μM) of Mg (Mengutay et al. 2013). S-deficient plants were reported with decreased chlorophyll contents under heat stress (Mobin 2010; Astolfi et al. 2003). A comparison between S-deficient and S-enriched plants showed that growth and plant biomass were increased with the satisfactory application of S under heat stress (Mobin et al. 2017). ROS generation reduced by alleviating the oxidative stress with S application in plants under heat stress.

The defense system of the plant is enhanced against the heat stress by maintaining the turgidity of the membrane with the help of Zn (Graham 2004). Heat stress effects were minimized with a satisfactory amount of Zn, while the growth parameters were reduced with allowable amount of Zn (Peck and McDonald 2010). Higher sensitivity toward heat stress was observed in plants with low Zn. N application controls the optimum nutrient accumulation in plant during the high temperature or heat stress (Demmig-Adams et al. 2014; Zhao et al. 2008). Chlorophyll contents, stomatal conductance, and photosynthetic rate in wheat seedling were also increased under heat-stressed plant with the appropriate amount of nitrogen (Hassan et al. 2015). However, effects of high night temperature on yield and growth of rice crop were not minimized by N application (Shi et al. 2016). Lipid thermal stability in cell membrane under the heat stress is associated with optimum application of Si. In addition, the negative effects of heat stress were also minimized by enhancing activities of enzymes of antioxidants and transpiration rate through Si application (Soundararajan et al. 2014; Rizwan et al. 2012; Agarie et al. 1998).

21.4 Conclusion

Biochemistry, phenology, anatomy, and morphology of plants are affected by the heat stress. Aggregation and denaturation of protein and rise in the fluidity of membrane in plants are directly associated with high temperature. Protein synthesis inhabitation and degradation of protein and mitochondrial enzymes as well as chloroplast are inactivated indirectly by high temperature. Crop yield reduction occurs under low temperature by affecting the pollen sterility, oval abortion, and fruit set reduction during reproductive phase. Therefore, it is indispensable to reduce the effects of heat stress through effective and efficient nutrient management in crop production. The acceleration of energy in stressed plants results in increased chloroplast memebrane damage and photooxidative effects, which in turns results in increased generation of reactive oxygen species (ROS) under high temperature.

Catalase, superoxide dismutase (SOD), and peroxidase (POD) antioxidants are increased, and reduction occurs in ROS with the application of N, Ca, K, and Mg in plant cells. The rate of photosynthesis and stability of chloroplast membrane are also increased by the optimum application of nutrients in plants. The plant body temperature is also maintained by the Ca and K intake which in turn facilitates the regulation of stomata and osmotic adjustment. Additionally, the maintenance of high tissue water potential under heat stress is also facilitated by the application of nutrients. In plants, the activation of biochemical, metabolic, and physiological processes reduces the heat stress with the application of micronutrients like Se and B. Due to less availability of literature on the importance of nutrients to reduce the heat stress, more research is required in the future for better understanding of plant system and heat stress with nutrient uptake.

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Chapter 22
Molecular Approaches to Nutrient Uptake and Cellular Homeostasis in Plants Under Abiotic Stress

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Abstract Plants suffer from abiotic stress due to several soil- and environment-related factors. They need water and essential plant nutrients to carry out their metabolism and survive. Plant genome regulates expression of different sets of genes to ensure availability of nutrients and water under conditions of stress and maintain their cellular homeostasis. The plasma membranes of root hair cells have several channels, which contain transporter proteins, coded by their specific genes for uptake of water and each of the essential plant nutrients. The transporter proteins involved in water uptake are known as aquaporins (AQPs). Since plants encounter several water stress conditions during its growth period, plant genome has many AQP genes to maintain cellular water homeostasis. Two sets of genes regulate uptake of primary nutrients, nitrogen, phosphorus, and potassium. A set of high-affinity transporters are involved, when their concentration in the growth medium is low, and a set of low-affinity transporters at higher concentrations. There are specific transporters for uptake of secondary and micronutrients both under low- and high-nutrient stress conditions. Plant genome responds to various types of abiotic stresses such as cold, heat, salinity, drought, and oxidative stresses and regulates suitably uptake of nutrients to maintain their cellular homeostasis. Amino acids, plant growth regulators, intermediate metabolites, and the nutrients themselves are involved in induction or repression of transporter-encoding genes as well as post-transcriptional modification of transporter proteins. Transcription factors regulate expression of nutrient stress response genes and control nutrient homeostasis in plants at molecular level. miRNAs are involved in posttranscriptional regulation of gene expression and also in nutrient stress signal transduction pathways. Some of the beneficial elements such as Na and Si play significant roles in abiotic stress tolerance of plants. Heavy metals, which are toxic and have no known function in plant metabolism, are sometimes taken up by ion transporters involved in uptake of essential nutrients from mineral-rich soils. Plants take up radioactive isotopes without any apparent damage to them. Exposure to high nuclear radiations may kill

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some of the plants but others survive. Abiotic stress caused by climate change has its effect on nutrient uptake by plants.

Keywords Aquaporins · Nutrient transporters · Transcription factors · miRNA · Beneficial elements · Radioisotopes · Climate change

22.1 Introduction

Plants suffer from abiotic stress both due to deficiency and excessive presence of plant nutrients. Other causes of abiotic stress include the presence of heavy metals; availability of micronutrients above or below their threshold concentrations; unsuitable soil conditions (mineral-rich soils, saline and alkaline soils, submerged or desert soils) coupled with unfavorable weather conditions, such as drought, excessive rain, high temperature, and cold waves; and more recently high concentrations of greenhouse gases and pollutants in the atmosphere. There are plants with special mechanisms, which can grow under all such adverse situations. Cultivated plants including domesticated crops when grown under these conditions suffer from abiotic stress, since two of their important functions, uptake of water and nutrient ions, are impeded and sometimes replaced by toxic ions leading to disruption of their metabolism. Most of the plants have however inbuilt defense mechanism to withstand reasonable variation in their optimal growth conditions, which cause abiotic stress (Marschner 1995; Hall 2002; Hasanuzzaman et al. 2012, 2013).

To cope with wide variations in concentrations of nutrient ions in the soil, plants have developed special mechanisms for net intake of a nutrient according to their need for this element rather than its concentration in the rooting medium (Imsande and Touraine 1994). The plasma membrane of cells contains a large number of channels, which are specific for water, nutrient ions, or other molecules and restrict any other type to pass through them. Such selectivity is caused by intrinsic transmembrane transporter proteins with fixed topology, lodged inside the channels. Cellular ion channel proteins are large molecules with multiple transmembrane α-helices. Channels alternate between open and closed conformations (gating) and allow water, ions, and other molecules to pass through them (The Nobel Prize in Chemistry 2003; Dubyak 2004; Diwan 2007).

There are different groups of genes for every nutrient and for water and other neutral molecules. These genes encode mRNA transcripts for translation of transporter proteins whose functions are to acquire the specific nutrient/water from the soil and transport it across the plasma membrane of the root hair cells and also within the symplasm. Different sets of genes specific for each nutrient at low and high concentrations are expressed for transport of every nutrient ion (Hammond et al. 2004; Rodriguez-Navarro and Rubio 2006). When the ionic concentration becomes toxic, plants adopt different mechanisms at physical, genetic, and biochemical level to maintain cellular homeostasis and survive (Marschner 1995; Hall

2002). There are also similar survival strategies at extremely low ionic concentrations (Fang et al. 2009; Lynch 2011; Plaxton and Tran 2011). Extensive research has been carried out on different types of plants on their survival strategies under adverse ionic environments often superimposed by hostile environmental stress (Ho et al. 2009; Fang et al. 2009).

22.2 Water and Ion Uptake and Homeostasis

22.2.1 Water Uptake

Water is fundamental to all life processes on earth. It is the universal solvent for living cells. Plants take up all the mineral nutrients through their roots in ionic forms in aqueous medium.

22.2.1.1 Mechanism of Water Uptake

Water is taken up into cells through water channels. Aquaporins (AQPs), a large protein family found in both eukaryotes and prokaryotes, control movement of water through the narrow channels located on the plasma membrane. The peptide sequence of a number of aquaporins (AQPs), their three-dimensional structures, and the corresponding DNA sequence have been determined. Plant AQPs appear to have the same general structure as mammalian AQP1 (Daniels et al. 1999). AQPs generally exist as tetramers. Each of the four monomers independently operates as water channels, but tetramerization gives them a synergistic benefit along with forming a central channel, which allows passage of gas molecules. The central channel may conduct ions through cGMP-mediated activation. This is probably caused by arginine-rich cytoplasmic D loop (The Nobel Prize in Chemistry 2003).

In addition to water, uncharged molecules with proper orientation, such as urea, glycerol, NH_3, $CO_{2,}$ metalloids, boron and silicon, and reactive oxygen species (ROS), are selectively allowed to pass through the water channels (Maurel et al. 2015). Ions carrying charges such as (H^+) and (H_3O^+) are prevented from passage. Glycerol molecules, which are larger than water molecules, appear to move in a single file through the amphipathic water channels, where NPA motifs of AQPs play a critical role (Chaumont et al. 2001).

22.2.1.2 Plant Aquaporins (AQP) and Cellular Homeostasis of Water

Plants maintain water balance under extreme water regimes during the growth period, such as drought and flooding, under variable weather conditions involving fluctuations of light, temperature, and nutrient stress. Plant genomes therefore contain a large number of aquaporin genes to regulate water transport across the plasma membranes. *Arabidopsis* has 38 aquaporin genes of 2–3 kb size (Johanson et al. 2001; Quigley et al. 2002), maize 33 (Chaumont et al. 2001), barley 23 (Katsuhara et al. 2002), rice 34 (Nguyen et al. 2013), wheat 35 (Forest and Bhave 2008), and soybean 66 (Zhang et al. 2014).

The AQP proteins belong to a major intrinsic protein (MIP) family, which are further classified into five subfamilies such as PIP, plasma membrane intrinsic protein; TIP, tonoplast intrinsic protein; NIP, NOD26-like intrinsic protein; SIP, small basic intrinsic protein; and XIP, X intrinsic protein, a poorly understood protein probably involved in transport of hydrophobic molecules (Venkatesh et al. 2015). Mosses (*Physcomitrella patens*) have two additional subfamilies, the hybrid intrinsic proteins (HIPs) and GlpF-like intrinsic proteins (GIPs).

Apart from water, plant aquaporins can transport several other molecules. PIPs and TIPs are efficient water channels, but PIPs can also transport H_2O_2 and CO_2 (Bienert and Chaumont 2014), whereas TIPs transport NH_3 and urea (Hooijmaijers et al. 2012). NIPs show less water transport activity but can transport metalloids such as B, Si, Se, As, and Sb. While the first three are considered as essential and beneficial elements, the last two are toxic to plants. SIPs show moderate water transport activity. XIPs are multifunctional, permeable to water, metalloids, and ROS (Maurel et al. 2015).

Members of subfamilies are not necessarily found in the locations as their names signify. The subfamilies are further subdivided into groups. In *Arabidopsis* PIP2;2 and PIP2;4 are exclusively expressed in roots and siliques (Quigley et al. 2002). At early tillering and panicle initiation stages in rice, 6 genes including *OsPIP2;4* and *OsPIP2;5* are predominantly expressed in roots, 14 genes including *OsPIP2;7* and *OsPIP1;2* are expressed in leaf blades, and 8 genes including *OsPIP1;1* and *OsTIP4;1* are evenly expressed in leaf blades, roots, and anthers. OsPIP2;1 and OsPIP3;1 have distinct role in developing rice grains (Hayashi et al. 2015). Wheat has 24 PIPs and 11 TIPs (Forest and Bhave 2008).

Plant aquaporins are localized throughout the cell secretory system including ER, Golgi, endosomes, autophagosomes, and vacuoles. Some isoforms are expressed in chloroplast. Aquaporins seem to be excluded from mitochondria and peroxisomes (Maurel et al. 2015).

22.2.1.3 Drought Stress and Aquaporins

It was observed from a study on response of salt and water stress and of phytohormones on aquaporin isoforms in radish seedlings that RsPIP2 groups of proteins were suppressed, when exposed to stress, but RsTIPs remained unchanged (Suga et al. 2002). In *Arabidopsis*, under drought stress, most PIPs and some TIPs had a high level of expression, while NOD26-like proteins (NIPs) were present at a much lower level. PIP transcripts were generally downregulated upon gradual drought stress in leaves, with the exception of AtPIP1;4 and AtPIP2;5, which were upregulated. AtPIP2;6 and AtSIP1;1 were constitutively expressed and not significantly affected by the drought stress (Alexandersson et al. 2005).

In most of the plants, PIPs predominantly present in plasma membrane, and TIPs, in the tonoplast, regulate water uptake. High water channel activity was found in rice, when OsPIP2;4 or OsPIP2;5 of rice were expressed in yeast. This did not happen when OsPIP1;1 and OsPIP1;2 were similarly expressed in yeast (Sakurai et al. 2005). Several studies on *Arabidopsis* in response to drought stress have shown that PIPs, which are highly expressed in roots, are most responsive to drought stress and most of them undergo transcriptional downregulation (Afzal et al. 2016). Downregulation of PIPs probably prevents water loss and backflow of water from plants to the drying soil. TIPs play key role in maintaining cellular homeostasis of water by transporting water from vacuole to the cytoplasm. Under salt stress, similar expressions of transcripts of PIPs and TIPs have been observed in most of the plants to conserve water within the cell (Afzal et al. 2016). Transgenic plants overexpressing aquaporins have been found to have better drought tolerance. A PIP2 subgroup gene of AQP, designated asTaAQP7, conferred drought stress tolerance in transgenic tobacco by increasing its ability to retain water, reducing ROS accumulation and membrane damage, and enhancing the activities of antioxidants (Zhou et al. 2012). A number of studies have shown that overexpression of *AQPs* enhances the ability of plants to tolerate abiotic stress by improving water use efficiency and hydraulic conductivity and retaining better water status. VfPIP1 isolated from *Vicia faba* leaf epidermis and expressed in transgenic *Arabidopsis* (induced by abscisic acid (ABA)) has been found to improve drought resistance of the transgenic plants by promoting stomatal closure under drought stress (Cui et al. 2008). Closure of stomata is an important mechanism to reduce water loss. This however effects conductance of CO_2 and reduction in photosynthesis. Aquaporins play an important role in the transport of water as well as CO_2 through cell membranes. A tobacco aquaporin NtAPQ1 has been found to be involved in mesophyll CO_2 conductance (Flexas et al. 2006). In tobacco and tomato plants, constitutive overexpression of NtAQP1 increased net photosynthesis, mesophyll CO_2 conductance, stomatal conductance and, under water stress, increased root hydraulic conductivity (Lpr) as well.

22.2.1.4 Salt Stress and Aquaporins

One of the primary responses of plants to salt is inhibition of their root water uptake capacity (i.e. root hydraulic conductivity, *L*pr). In a study on early effects of salt stress on aquaporins, it was observed that in *Arabidopsis* all PIP and TIP aquaporin transcripts with a strong expression signal showed a 60–75% decrease in their abundance between 2 and 4 h following exposure to salt. Aquaporins contribute to >80% of *L*pr, and therefore most of salt-induced inhibition of water uptake is probably caused by significant decrease of their expression (Bourssiac et al. 2005).

22.2.1.5 Regulation of Water Uptake by Aquaporins

Plant aquaporins have developed special mechanisms to regulate water flow under adverse water regimes such as drought, flooding, and salt stress. Such conditions trigger certain cellular signals (dephosphorylation and change of pH), which close the channel and restrict water flow. A study on spinach plasma membrane aquaporin SoPIP2;1 on cellular mechanism of water flow through membrane under adverse water regime showed that channel closure resulted either from the dephosphorylation of two conserved serine residues under conditions of drought stress or from the protonation of a conserved histidine residue following a drop in cytoplasmic pH due to anoxia during flooding. A cytoplasmic loop occludes and physically blocks the channel entrance from cytoplasm, through a molecular gating mechanism. Phosphorylation removes the loop from the channel and allows reentry of water. This mechanism is probably conserved in all plasma membrane aquaporins (Törnroth-Horsefield et al. 2006).

22.2.2 Nutrient Stress and Ionic Homeostasis

Both suboptimal and toxic concentrations of plant nutrients in the growth medium of plants cause nutrient stress. Plants maintain an optimal concentration of nutrient ions and pH in its cytoplasm for its metabolism irrespective of their concentrations in the growth medium. Excessive nutrients absorbed by the plants are deposited in the apoplast. Any nutrient getting through the plasma membrane is transported to the vacuole to maintain ionic homeostasis in the cytoplasm.

22.2.2.1 Mechanisms of Nutrient Uptake

There are many channels in the plasma membrane, each adapted to allow passage of one specific ion or molecule and not others. The transporter proteins located inside these channels are divided into two classes: (1) ion channel proteins and (2) ion transporter proteins.

Channel proteins are large molecules with multiple transmembrane α-helices. They alternate between open and closed conformations (gating). There is conformational change of the channel protein due to any one of the extrinsic factors, such as (i) changes in membrane potential, (ii) binding of a small regulatory molecule, or (iii) membrane stretch (e.g., via link to the cytoskeleton) (Dubyak 2004; Rainer 2012). These factors determine if the channel is in a gated state (open for transport) or closed state (incapable of ion transport). Extrinsic factors control the accessibility of ions to the channel domain, which acts as a pathway for movement of ions from one side of the plasma membrane to the other side. Since there are no energetic interactions, between channel protein and the transported ion, the rate of transport of ion is fast. There is probably no binding site within the channels to restrict their movement. Even if they exist, they are shallow and separated by small free energy barriers (Roux et al. 2011).

All channels mediate passive transport of ions down their chemical or electrochemical gradient across the membrane due to difference in concentrations of ions on each side of the membrane as well as any electrical potential across the membrane.

22.2.2.2 Ion Transporter Proteins (Carriers)

Transporter proteins are "vectoral" enzymes (Dubyak 2004). Their functioning involves (i) a selective recognition/binding of the ion to be transported, (ii) conformational changes in carrier protein due to binding of the ion, and (iii) physical movement of the ion across the membrane caused by such conformational changes. Ion transporters can catalyze movement of ions against their electrochemical gradient (not ion channels) deriving energy from ATP hydrolysis. There are three types of ion transporters:

(i) *Uniporters*: They transport one type of ion across the membrane, e.g., P-type ATPases, Ca^{2+}-ATPase.
(ii) *Symporters (cotransporters)*: They transport more than one type of ion across the plasma membrane, e.g., NRTs ($2H^+/NO_3^-$ cotransport), TaHKT1 (K/Na cotransporter).
(iii) *Antiporters (exchangers)*: There is exchange of one ion for the other, which moves in opposite directions, e.g., CHX (K^+/H^+ antiporter), CAX (Ca^{2+}/H^+ antiporter).

Furthermore, it is good to recall that ion channels are not really designed to keep ions in place, but to allow them to diffuse rapidly across the membrane. Therefore, it is likely that binding sites inside the channel, even when they exist, should be rather shallow and separated by small free energy barriers (Roux et al. 2011).

22.3 Primary Nutrients

Nitrogen (N), phosphorus (P), and potassium (K) are required in relatively larger quantities for growth and metabolism of plants. Most of the soils globally are deficient in one or more of these elements and the available nutrients are not sufficient to meet the crop requirement. Hence nutrient stresses caused by them are mostly due to their suboptimal presence rather than toxicity.

There are generally two types of ion transporters involved in uptake of nutrient ions through the plasma membrane of cells. The "low-affinity" transporters are involved in ion uptake when the concentration of the ion in the growth medium is high, and high-affinity transporters operate when the concentration is low. Low-affinity transporters are generally constitutive in nature.

22.3.1 Nitrogen

Plants contain about 1–6% of N of their dry weight. Nitrogen is primarily taken up by plants as NO_3^-or NH_4^+ ions. Unfertilized soils may contain NO_3^- at a concentration of <1 mM, but application of fertilizers may raise it >70 mM. Concentration of N is more or less constant within cytoplasm. Nitrate concentration in cytoplasm is limited to about 2–5 mM and 5–75 mM inside vacuole (Miller and Smith 1996). $NH_4^+$is toxic and is not allowed to accumulate within the plants.

The primary event of NO_3^- uptake is its transport through plasma membrane of root epidermal and cortical cells. This is carried out by a favorable H^+ (proton) electrochemical gradient maintained by the plasma membrane (PM) H^+-ATPases (proton pumps) (Miller and Smith 1996; Quaggiotti et al. 2003; Sperandio et al. 2014). (PM) H^+-ATPase activity maintains membrane potential ($\Delta\Psi$) and proton-motive force (Δp) necessary for ion transport. For both high- and low-affinity transport system, NO_3^- uptake takes place by symport of $2H^+/NO_3^-$ (Crawford and Glass 1998).

22.3.1.1 Nitrate Transport Genes

The genes involved in transport of NO_3^- across plasma membrane in *Arabidopsis* are (1) *NRT1* (nitrate transporter1/peptide transporter family, 53 members), (2) *NRT2* (7 members), (3) *CLC* (chloride channel, 7 members), and (4) *SLAC1/SLAH* (slow anion channel-associated 1 homologs, 5 members) (Krapp et al. 2014). The four families have a total of 73 genes out of which 60 are from *NRT1/PTR* and *NRT2* families. Out of 35 genes characterized, 24 are nitrate transporters.

22.3.1.2 Nitrate Transporters (NRTs) in Plants

When the external NO_3^- concentration is high (1–50 mM), an essentially unregulated and constitutively expressed low-affinity transport system (LATS) operates (Crawford and Glass 1998). A high-affinity transport system (HATS) operates, when external NO_3^- concentration is low (<0.2 mM). Some of them are constitutively expressed (cHATS) and others induced by NO_3^- (iHATS) (Fig. 22.1).

The *NRT1* genes encode low-affinity transporters (LATS), when the NO_3^- concentration in the soil is high >1 mM (Orsel et al. 2002). The *NRT2* genes encode high-affinity nitrate transporters at low NO_3^- concentration (<0.2 mM). Some of the *NRT2* genes are inductive (*iHATS*) and others constitutive (*cHATs*). AtNRT1; 1 (CHL1) is a dual-affinity nitrate transporter, switched off and on by phosphorylation/dephosphorylation of threonine T101 in its polypeptide chain (Liu et al. 1999). The CBL (calcineurin B-like)-interacting protein kinase, CIPK23 (SnRK3;23), phosphorylates T101 under low nitrate conditions, allowing NRT1;1 to act as a

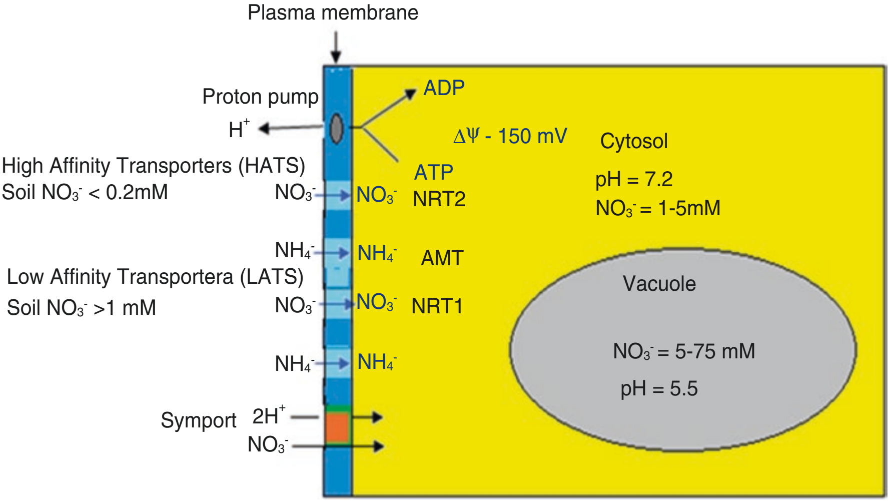


Fig. 22.1 Mechanism of nitrogen uptake and cellular homeostasis in plants. (Adapted from Mitra 2015, 2017)

high-affinity nitrate transporter (Ho et al. 2009). Dephosphorylated NRT1;1 is a low-affinity nitrate transporter.

Nitrate transport in *Arabidopsis* is carried out by two transporters from NRT1 family, AtNRT1;1 and AtNRT1;2, and two from NRT2 family, AtNRT2;1 and AtNRT2;2. When external NO_3^-concentration is low, NRT2;1 proteins localized on the plasma membrane constitute the major component of HATs (72%) activity (Li et al. 2007). It requires a second protein NAR2 for its stability. AtNRT2;1 and AtNAR2;1 form a tetramer with two subunits each, which constitute the active NO_3^- transporter (Yong et al. 2010).

In higher plants *NRT2* genes isolated so far are preferentially expressed in the roots (Tsay et al. 2007). OsNRT1 expressed in epidermal cells of rice roots is a homolog of *Arabidopsis* AtNRT1;1(CHL1) (Lin et al. 2000). Four HATs OsNRT2;1, OsNRT2;2, OsNRT2;3, and OsNRT2;4 and two NAR proteins OsNAR2;1 and OsNAR2;2 have been isolated from rice (Feng et al. 2011, Sperandio et al. 2014). In maize ZmNRT2;1 is involved in influx activity and ZmNRT2;2 in xylem loading process (Trevisan et al. 2008).

22.3.1.3 The AMT1 Family of Ammonium Transporters

High-affinity NH_4^+ transporter in *Arabidopsis* contain five members, of which AtAMT1;1, AtAMT1;2, and AtAMT1;3 have been studied in detail. In rice four NH_4^+ transporter genes have been identified (Suenega et al. 2003). OsAMT1;1 is expressed in roots and shoots. OsAMT1;2 is root-specific and induced by NH_4^+. OsAMT1;3 is root-specific and depressed by nitrogen application (Sonoda et al.

2003). Two rhizodermis-localized transporters ZmAMT1;1 and ZmAMT1;3 have been identified from maize.

22.3.1.4 N Regulatory Network

An intricate N regulatory network at the root tip is responsible for orchestrating changes in root growth rate and root architecture. Nitrate stimulates primary root growth, both directly and by antagonizing inhibitory effect of glutamine, which stimulates root branching (Walch-Liu and Forde 2008). Some of the genes encoding nitrate transporters are subjected to transcriptional regulation through inductive effects of NO_3^-, while both encoding NO_3^- and NH_4^+ transporters are subject to downregulation by glutamine (Anthony et al. 2002).

Ammonium transporters are oligomeric proteins. They undergo conformational coupling among monomers for ammonium uptake. This provides a mechanism for tight regulation of ammonium transporters. Rapid shut-off mechanism is required to prevent toxic accumulation of NH_4^+. Application of higher levels of NH_4^+ blocks NO_3^- uptake by roots (Mitra 2017).

22.3.1.5 NH_4^+ and Al Tolerance

Ammonium is preferred by aluminum-tolerant rice varieties, whereas Al-sensitive ones prefer nitrate. According to Zhao and Shen (2013), N signaling molecules produced during N uptake and assimilation may be involved in the Al tolerance of rice, and the regulation of N metabolism by Al may be one of the factors in the beneficial role of Al in some plants. The interactive regulation of N and Al seems to facilitate the growth of plants in acid soils.

Functional disruption of nitrate transporter, NRT1;8, has been found to decrease Cd tolerance (Li et al. 2010), whereas that of NRT1;5 increase Cd tolerance (Chen et al. 2012) in *Arabidopsis thaliana*, indicating an important role of nitrate in regulating metal tolerance.

22.3.1.6 Nitrogen Uptake, Aquaporins, and Water Stress

Aquaporins have a significant role in N absorption, N mobilisation, N detoxification, and N metabolism in higher plants. The PIP, TIP, and NIP subfamilies are involved in transport of NH_3 and urea.

High N application to rice has been reported to result in increased transcription level of aquaporins, increased rate of water uptake and the root hydraulic conductance and decreased aerenchyma formation (Ren et al. 2015).

Nitrate (NO_3^-), the major form in which N is taken up by plants, exerts beneficial effects on root water uptake in numerous plant species. Limited NO_3^- availability has been reported to result in a dramatic (20–50%) reduction in root hydraulic conductivity (Lp_r) in a number of plants such as *Arabidopsis* (Li et al. 2016), sunflower (Gloser et al. 2007), maize, wheat (Carvajal et al. 1996), lotus (Clarkson et al. 2000, Prosser et al. 2006), and rice (Ishikawa-Sakurai et al. 2014). According to Li et al. (2007), the nitrate transporter AtNRT2; 1 is responsible for 72% of HATs activity in *Arabidopsis* at low NO_3^- concentration. NO_3^- also acts as a signaling molecule and as a sensor (Krapp et al. 2014). NRT2.1, a high-affinity nitrate transporter, has been suggested as a nitrate sensor involved in the regulation of lateral root formation (Little et al. 2005). Recent studies by Li et al. (2016) suggest a strong relationship between Lp_r and plant NO_3^- accumulation, together with a specific role for the high-affinity NO_3 transporter NRT2.1 in determining Lp_r. Four *PIP* genes, *PIP1;1*, *PIP1;2*, *PIP2;1*, and *PIP2;3*, show a strong positive correlation between their transcript abundance and Lp_r (Li et al. 2016).

Nitrate has been shown to alter aquaporin expression in tomato (Wang et al. 2001). Studies on rice indicate that N deprivation decreases the expression of root-specific aquaporin genes, whereas N resupply increases their expression. Changes in aquaporin gene expression have been correlated with changes in hydraulic conductivity. N deprivation has been found to increase dry matter allocation to the roots. In a split-root experiment, the expression of root-specific aquaporin genes was downregulated in the N-deprived half, whereas it was upregulated in the N-supplied half (Ishikawa-Sakurai et al. 2014).

22.3.1.7 Nitrogen Stress and microRNA

Gene expression can be regulated at the posttranscriptional level through small RNAs such as microRNAs (miRNAs) and small interfering RNAs (siRNAs) (Bakhshi et al. 2016). Plant microRNAs play critical roles in most of the biological processes such as development, differentiation, and plant responses to biotic and abiotic stress (Lelandais-Brière et al. 2010).

microRNAs (miRNAs) containing 19–25 nucleotides are found in all animals and plants but not in fungi. They are posttranscriptional regulators encoded by specific genes, several at a time or by some portions of the introns of genes, whose mRNA they regulate. They either completely destroy the mRNA if their sequences exactly match (usually in plants) or repress the translation of mRNA if there is a partial match. In the latter, several of them simultaneously bind to the UTR (untranslated) region of mRNA. In plants, they may target the coding region itself (He and Hannon 2004).

Recent studies indicate that miRNAs regulate plant adaptive responses to nutrient deprivation (Zhao et al. 2011). miR169 is a conserved plant miRNA that is found in diverse plant species. The expression of miR169 is downregulated in *Arabidopsis* due to N starvation. The precursor of miR169, *MIR169a*, is substantially downregulated in both roots and shoots by N starvation. *miR169* has been reported to regulate symbiotic nodule formation in *Medicago truncatula*, and overexpression of *MIR169a* leads to a developmental block of nodule formation (Combier et al. 2006)**.**

Liang et al. (2012) studied the small RNA population in *Arabidopsis* grown under N-sufficient and N-deficient conditions. They observed that due to N starvation, the expressions of miR169, miR171, miR395, miR397, miR398, miR399, miR408, miR827, and miR857 were repressed, whereas those of miR160, miR780, miR826, miR842, and miR846 were induced. Several of these miRNAs were probably involved in cross talk in response to deficiencies of other nutrients such as N, P, Cu, and S (Liang et al. 2012). Wang et al. (2013a, b) reported that a total of 150 known miRNA variants as well as 2 novel miRNAs were identified to be responsive to low N stress in two soybean genotypes. Xu et al. (2011) performed a genome-wide search to detect miRNAs responding to the chronic and transient nitrate-limiting conditions in maize. Nine miRNA families (miR164, miR169, miR172, miR397, miR398, miR399, miR408, miR528, and miR827) were identified in leaves, and nine miRNA families (miR160, miR167, miR168, miR169, miR319, miR395, miR399, miR408, and miR528) were identified in roots. The majority of miRNAs gave different responses to chronic and transient nitrate-limiting conditions. Once the concentration of nitrate was normalized, they returned to their base values. In rice N starvation represses expression of miR3979. It is plausible that under nitrogen starvation conditions, downregulation of miR3979 induces tryptophan biosynthesis, followed by increased auxin production, resulting in lateral root initiation to absorb more nitrogen from the soil (Jeong et al. 2011). miRNAs appear to play a key role in low-N tolerance by crop plants (Shriram et al. 2016).

22.3.2 Phosphate (Pi)

Plants contain 0.05–0.5% of phosphate. While soil availability of Pi rarely exceeds 2 μM, the concentration of Pi in root cells is 2–20 mM (more than 10,000-fold higher than Pi in the soil solution). Plants have both high- and low-affinity phosphate transporters, which are $H_2PO_4^-/H^+$ symporters. The low-affinity transport systems are constitutive and operate at higher Pi concentration. High-affinity phosphate transporters are located primarily in plasma membrane of root hair cells and operate at low Pi concentration. The high-affinity transporters are induced when Pi is deficient. Transport against the steep concentration gradient takes place through active transport with energy derived from ATP. The movement from root surface to xylem is symplastic and is at a rate of about 2 mM h^{-1} (Bieleski 1973). Transport of Pi to above ground parts is through xylem flow and to cells in tissues through symplastic transport. Movements of Pi through plasma membrane into cells and into vacuole within cells are carried out by $H_2PO_4^-/H^+$ symporters with energy derived from ATP (Ullrich and Novacky 1990; Mitra 2015).

Phosphate deficiency results in coordinated induction of hundreds of genes encoding enzymes, which maximize capacity of plants to acquire phosphate more efficiently from external sources and reprioritize internal use of phosphorus (Plaxton and Tran 2011).

22.3.2.1 Genes Involved in Pi Uptake by P-Stressed Plants

Micro- and macro-array analysis of P-stressed plants has shown transcript abundance of a number of genes with homology to Pi transporters, organic acid synthesis, purple acid phosphatase, multidrug and toxin efflux (MATE), transcription factors, signaling, and defense (Tesfaye et al. 2007). Based on the sequence identity and their varied subcellular localization, plant Pi transporters are grouped into five phylogenetically distinct classes of families: PHT1, PHT2, PHT3, PHT4, and PHT5. Members of PHT1 gene family are expressed in root epidermal cell, and the encoded transporters are located on the plasma membrane (Lin et al. 2009). They are high-affinity $H_2PO_4^-/H^+$ symporters and function to acquire Pi from the rhizosphere. Members of PHT2 gene family are found in chloroplasts (Versaw and Harrison 2002); members of PHT3 family are located in mitochondria (Poirier and Bucher 2002) and of PHT4 family located in non-photosynthetic plastids or the Golgi apparatus (Guo et al. 2008). PHT5 is located in the vacuole. The members of PHT1 family in *Arabidopsis* with 12 transmembrane domains have different functions: the Pht1;4 involved in Pi acquisition and Pht1;1 in Pi accumulation in shoots during Pi sufficiency due to its role in xylem loading process (Fang et al. 2009; Lin et al. 2009). Orthologous genes of Pht1;1 have been found in barley, rice, maize, potato, and *Medicago truncatula* sharing the same expression pattern and their basic role in Pi uptake. Pht2;1 is the only member of PHT2 family in *Arabidopsis*, which is highly expressed in leaves but scarcely found in roots. It is located in chloroplast and encodes low-affinity Pi transporters.

Genes that respond to P deficiency can be grouped into “early genes” that respond rapidly and often nonspecifically to Pi deficiency or “late genes” that impact on the morphology, physiology, or metabolism of plants upon prolonged Pi deficiency (Vance et al. 2003; Hammond et al. 2004). There is a Pi starvation-inducible rescue system in plants with their promoter region, the *PHO* regulon genes, under a common regulatory system (Goldstein et al. 1988). The Pi-responsive genes, *TPSI1* from tomato and *Mt4* from *Medicago truncatula*, have cis-regulatory elements “GCACG (G/T)” in their binding sites. The *AtPHR1* (phosphate starvation response 1) gene from *Arabidopsis* has a motif, a *cis*-element “GNATATNC” (P1BS, *PHR1*-specific binding sequence, *cis*-element “GNATATNC”), which is shared by several Pi-responsive genes. The motif “P1BS” (GNATATNC) is recognized by the transcription factor *PHR1*, which binds as a dimer to the motif (Rubio et al. 2001). Overexpression of *PHR1* results in increased concentration of Pi in the shoots along with an elevated expression of a large number of Pi-deficient genes encoding Pi transporters, phosphatases, and RNase (Nilsson et al. 2007). *PHR1* appears to be a key transcriptional activator, which controls Pi uptake and distribution within the plant, anthocyanin accumulation, and carbon metabolism. The two homologs *PHR1*, identified in rice, *OsPHR1* (*Oryza sativa* phosphate limitation-inducible gene 1) and

OsPHR2, control expression of several Pi starvation-induced genes (Zhou et al. 2008).Overexpression of *OsPHR2* results in increased Pi accumulation in shoot, root elongation, and root hair proliferation in transgenic rice. *PHR1* is involved in coordinated regulation of many "late" Pi starvation genes, such as of RNases, phosphatases, TPSI/Mt4 family (Franco-Zorrilla et al. 2004, Hammond et al. 2004), and *OPSI1* (Wasaki et al. 2006), which have *PHR1* binding sites. *PHR1* binds as a dimer to the promoter of "late" Pi starvation genes. Most of the Pi taken up by roots is subsequently transported through xylem to shoots. Phosphate transporters, OsPht1;2 and OsPht1;6 in rice, are involved in Pi translocation from roots to shoots (Ai et al. 2009).

22.3.2.2 Effects of Pi Deficiency on Plant Metabolism

Under conditions of Pi deficiency, plants recycle P from older tissues to new tissues. Plants also remobilize from nonessential uses to essential uses. Intracellular (vacuolar) acid phosphatases (with acidic pH optima) are upregulated by Pi deficiency, which remobilize Pi from internal phosphomonoesters and anhydrides. Some of the P-rich organic constituents of cells are replaced and utilized to conserve Pi. Membrane phospholipids in Pi-starved plants are replaced by amphipathic sulfolipids and galactolipids (Plaxton and Tran 2011).

Starch Accumulation Phosphate causes allosteric inhibition of the enzyme ADP-Glc pyrophosphorylase, involved in starch biosynthesis in cells. Phosphate deficiency removes such allosteric inhibition. This results in starch accumulation in the cell (Vance et al. 2003).

Synthesis of Anthocyanins A common symptom of Pi deficiency in plants is dark green or purple shoots. This is due to anthocyanin accumulation. Phosphate starvation causes induction of enzymes involved in synthesis of anthocyanins (Vance et al. 2003, Fang et al. 2009), which protect nucleic acids.

ATP Synthesis Under severe Pi-deficient conditions, a large decline (up to 80%) of ATP, ADP, and other nucleoside phosphates occurs. Plants respond by adopting alternative metabolic pathways for cytoplasmic glycolysis, mitochondrial electron transport, tonoplast H^+ pumping to facilitate respiration and vacuolar pH maintenance. Critical roles are played by pyrophosphate-dependent glycolytic bypass enzymes and metabolic Pi-recycling systems (Plaxton and Tran 2011).

Glycolysis Pi deficiency has been reported to significantly upregulate some of the glycolytic bypass enzymes such as pyrophosphate (PPi)-dependent phosphofructokinase, PPi-phosphoenol pyruvic kinase, pyruvate phosphodikinase, and tonoplast H^+ pyrophosphatase (Plaxton and Podesta 2006).

22.3.2.3 miRNA and Phosphate Deficiency

Phosphate deficiency causes upregulation of miR399, which decreases rapidly on Pi addition (Fujii et al. 2005; Bari et al. 2006). Overexpression of *Arabidopsis* miR399 in tomato results in increased accumulation of Pi. There is also augmented excretion of acid phosphatases and protons by roots, which facilitates Pi acquisition from soil (Gao et al. 2010). Homologs of miR399 have been found in rice, tomato, common bean (*Phaseolus vulgaris)*, and *Medicago truncatula* (Kuo and Chiou 2011). Apart from miR399, a number of microRNAs such as miR156, miR159, miR166, miR319, miR395, miR398, miR399, miR447, and miR827 have been identified from plants of different species, which are involved in Pi deficiency syndrome (Kuo and Chiou 2011). Most of these miRNAs are involved in signaling pathway for Pi deficiency. Some of the miRNAs involved in Pi deficiency have also been found to be affected by other plant nutrients. For example, miR169, miR395, and miR398, which are downregulated by Pi deficiency, are also similarly affected due to deficiency of N, K, Cu, Fe, or S. miRNAs involved in stress signal transduction pathways have considerable cross talk with different nutrient homeostasis (Kuo and Chiou 2011; Liang et al. 2012).

22.3.2.4 Pi Stress Response Genes and Transcription Factors (TF)

Several families of TFs, such as *MYB*, *SCARECROW*, *APETALA2* domain, homeobox, zinc fingers, and *WRKY*, are involved in expression of Pi stress response genes. Bioinformatic analysis of Pi-stressed tissues of legumes (*Medicago*, *Lupinus*, *Phaseolus*, and *Glycine*) indicates the presence of transcription factors, *WRKY, MYB*, and zinc finger families of genes (Graham et al. 2006). Database search has resulted in identification of 26 potential phosphate transporter gene families in rice. At 2 kb upstream region of these genes, 237 putative *cis*-elements have been found, most of which are phosphate-responsive or other stress-related regulatory *cis*-elements, such as PHO-like, TATA box-like, PHR1, or helix-loop-helix elements, and WRKY1 and ABRE elements (Liu et al. 2011).

Under Pi-deficient conditions, maize root shows altered expression of transcription factors, “SHORTROOT” and “SCARECROW-LIKE” TFs, which are involved in determining meristem identity and root morphology.

AtWRKY75, AtWRKY6, and AtWRKY42 transcription factors modulate phosphate (Pi) acquisition in *Arabidopsis*. AtWRKY75 is a modulator of Pi starvation response as well as root development (Devaiah et al. 2007; Jiang et al. 2017). As a plant-specific TF, WRKY has a conservative WRKYGQK domain at N terminal and a zinc finger motif. WRKY specifically combines with W box [TTTGAC(C/T)] in *PHT1* promoters and regulates the expression of *PHT1*.

A rice *OsWRKY74* TF belonging to group III of WRKY TF family, localized in the nucleus and mainly expressed in roots and leaves, is involved in phosphate starvation response. Overexpression of *OsWRKY74* results in increase of P, N, and Fe concentration and upregulation of cold stress-responsive genes (Dai et al. 2016).

A bHLH transcription factor involved in Pi stress in rice, *OsPTF1* (*Oryza sativa phosphate starvation-induced transport factor1*), has been cloned and characterized (Yi et al. 2005). Normally *OsPTF1* is constitutively expressed in shoots of rice plant. Under Pi stress conditions, transcript accumulation of *OsPTF1* is induced in roots.

HD-ZIP TF is involved in signaling expression of Pi-responsive genes in soybean (Tang et al. 2001).

The *Arabidopsis* MYB TF has sequence homology with *PHR1* (phosphate starvation response gene) of *Chlamydomonas reinhardtii* and binds to an imperfect palindromic consensus sequence "*5-GNATATNC-3*" (Rubio et al. 2001). Many Pi deficiency-induced genes such as *LaPT1 and LaSAP1* of white lupine have "*GNATATNC*" in their 5′ upstream region (Tesfaye et al. 2007).

Tesfaye et al. (2007) using semi-quantitative reverse transcription PCR analysis of 13 ESTs (partially sequenced cDNA inserts) encoding zinc finger transcription factors have reported that there is increased transcript abundance of two of the ESTs in Pi-starved roots of common bean. ZAT6 (zinc finger of *Arabidopsis* 6), a cysteine-2/histidine-2 zinc finger transcription factor, has been found to be responsive to Pi stress (Devaiah et al. 2007).

22.3.3 Potassium (K^+)

Plants contain 2–10% of K of their dry weight. Cytoplasmic concentration of K^+ is maintained at approximately 100 mM, although vacuole may contain 20–200 mM of K^+ (Gierth and Maser 2007). Apoplastic concentration of K^+ may vary between 10 and 200 mM and may increase up to 500 mM (White and Karley 2010; Wang et al. 2013a, b).

The pathways of potassium uptake by plants fall into several distinct categories. K^+ channels consist of three families:

(a) Shaker-type channels, KCO channels (a total of 15 genes in *Arabidopsis*) and cyclic nucleotide-gated channels (CNGC, 20 genes in *Arabidopsis*) (Very and Sentenac 2002)
(b) Trk/HKT transporters: [Na^+/K^+ symporter] (Schachtman 2000), one gene in *Arabidopsis*
(c) KUP/HAK/KT transporters: [H^+/K^+ symporter] (Kim et al. 1998), 13 genes in *Arabidopsis*
(d) K^+/H^+ antiporter homolog: six genes in *Arabidopsis*
(e) Glutamate receptors (GLRs): 20 genes in *Arabidopsis* (Very and Sentenac 2002)

22.3.3.1 KUP/HAK/KT Transporters

All plant genomes contain genes encoding KUP (potassium uptake permeases)/HAK (high-affinity potassium transporters)/KT (potassium transporters) (given different acronyms by different research groups) transporters (not found in *Protista* and *Animalia*). All KT/KUP/HAK transporters can be grouped into four distinct clusters. All plants have Cluster I or Cluster II transporters. Cluster III genes are found only in *Arabidopsis* and rice. Cluster IV is the smallest in number, which comprises only of four rice genes. *Cluster I transporters* have high affinity for K^+ and play a key role in potassium acquisition, when K^+ availability is low, e.g., *HvHAK1* in barley roots, *LeHAK5* in tomato, and *AtHAK5* in *Arabidopsis*. *Cluster II transporters* facilitate low-affinity K^+ transport complementing potassium channels. These transporters are localized in the tonoplast and facilitate K^+ efflux from the vacuole. Under conditions of K^+ deprivation, export of K^+ from the vacuole is mediated by a K^+/H^+ symporter with a 1:1 stoichiometry for the maintenance of K^+ homeostasis.

22.3.3.2 K^+/H^+ Antiporter Homologs

Also known as *CHX* (Cation/H^+ eXchanger), a member of the family, AtCHX17, expressed in the cortex and epidermis of the mature root is involved in K^+ acquisition and homeostasis rather than Na^+ transport.

22.3.3.3 Abiotic Stress and Intracellular K^+ Homeostasis

All abiotic and biotic stresses result in a significant disturbance to intracellular potassium homeostasis. K^+ response to plants under conditions of stress consists of controlling the activity of superoxide dismutase and mitigating injuries caused by free radicals of active oxygen species.

22.3.3.4 K^+ Channel Proteins and Aquaporins

Aquaporins and potassium channel proteins are critical for a plant to maintain proper cytosolic osmolarity in response to drought or other stresses. A study on rice (Liu et al. 2006) indicates that water channels and K^+ channels/transporters have potential functional correlations. The mRNA expression levels of plasma membrane intrinsic proteins (PIPs) and K^+ channel/transporters responded similarly to K^+ starvation or water deprivation. Transcription of the *PIP* and K^+ channel-encoding genes are induced by K^+ starvation and can be downregulated by polyethylene glycol (PEG)-mediated water deficit. Root hydraulic conductivity (*Lpr*) also increases during K^+ starvation.

Aquaporin phosphorylation seems to be a significant target in plants under stress (see Regulation of Water Uptake by Aquaporins). *At*PIP2;1 phosphorylation is decreased and increased, respectively, on exposure of *Arabidopsis* roots to salt (NaCl) or hydrogen peroxide (H_2O_2) (Prak et al. 2008).

22.3.3.5 Effect of K^+ on Drought Stress

Adequate availability of water for crop growth is one of the major constraints in arid and semiarid regions. The lack of supporting irrigation facilities in rain-fed agriculture causes crop failure around the world. However, plants have innate capacity to withstand reasonable drought conditions. There is a close relationship between drought tolerance and K^+ status of plants. Adequate amounts of K^+ can enhance the total dry mass accumulation of crop plants under drought stress in comparison to lower K^+ concentrations. This finding might be attributable to stomatal regulation by K^+ and corresponding higher rates of photosynthesis. It has been recently reported that (Carraretto et al. 2013) a thylakoid-located two pore K^+ channel TPK3 modulates the composition of proton-motive force (PMF) through ion counterbalancing to convert photochemical energy into physiological functions. In *Arabidopsis*, the channel is found in the thylakoid stromal lamellae. K^+ is also essential for the translocation of photo-assimilates and in root growth (Romheld and Kirkby 2010). Increased and appropriate K^+ supply promotes root growth in K-deficient soils. This increases the root surface that is exposed to soil and results in increased root water uptake (Romheld and Kirkby 2010). Lindhauer (1985) reported that K nutrition not only increased plant total dry mass and leaf area but also improved the water retention in plant tissues under drought stress.

Increased evidence shows that the maintenance of membrane integrity and stability under drought stress is also essential for plant drought tolerance. Cell membrane stability significantly declines under drought stress. In a study by Premachandra et al. (1991), maize plants with higher K applications showed greater adaptation to water stress. This improvement was mainly attributed to the role of K in improving cell membrane stability and osmotic adjustment ability. An adequate K supply is essential to enhancing drought resistance by increasing root elongation and maintaining cell membrane stability. K^+ uptake also improves drought resistance of crops by reducing leaf osmotic potential, increasing turgor, bound water content, and water use efficiency.

K^+ controls activity of superoxide dismutase (SOD) and mitigates possible injury from active oxygen derived from drought stress to plasma membrane. K^+ increases proline content of leaves and suppresses malondialdehyde (MDA) content (induced by drought) to strengthen drought resistance of crops. K^+ maintains the balance of internal hormone level of CTK, ABA, and ethylene.

22.3.3.6 K^+ Transporters and Salt Tolerance

Although plants have an absolute requirement for K^+, and Na^+ is toxic for many biological reactions in the cytoplasm, this does not apply to vacuolar processes (Flowers and Läuchli 1983; Subbarao et al. 2003). Na^+ can undertake osmotic functions, reducing the total K^+ requirements and improving growth when the lack of K^+ is a limiting factor.

HKT transporters (High-affinity K^+ transporter), which mediate Na^+-specific transport or Na^+-K^+ transport, play a key role in regulation of Na^+ homeostasis (Rodriguez-Navarro and Rubio 2006; Munns and Tester 2008). There is only one *HKT* gene in *Arabidopsis thaliana* (Uozumi et al. 2000) and eight genes in rice (Horie et al. 2001; Garciadeblas et al. 2003). HKT transporters are divided into two main subfamilies (Platten et al. 2006). Members of subfamily 1 have a serine residue in the first pore loop of the protein, which is replaced by glycine in most members of subfamily 2. The division is also associated with differences in Na^+ and K^+ selectivity (Horie et al. 2001; Maser et al. 2002; Garciadeblas et al. 2003). Gene members of subfamily 1 are all Na^+-specific transporters. Some of them are expressed in cells in the stele rather than the root cortex and regulate root-to-shoot transport of Na^+ by removing Na^+ from the xylem sap as it flows to the shoot. Members of subfamily 2 are Na^+-K^+ cotransporters or Na^+ and K^+ uniporters, except OsHKT2;2 (OsHKT2). Some of them are specifically expressed in the root cortex and may serve to scavenge Na^+ under conditions of K^+ deficiency and so provide ionic homeostasis. Under saline conditions the expression of those genes may be downregulated. *OsHKT2;1*mediates the transport of Na^+ into roots of K^+-starved plants and enhances their growth, but is downregulated when plants are exposed to 30 mM NaCl (Horie et al. 2007). TaHKT2;1 (TaHKT1) and HvHKT2;1 (HvHKT1) in wheat and barley roots mediate Na^+ uptake into roots of K^+-starved plants (Laurie et al. 2002; Haro et al. 2005).

22.4 Secondary Nutrients

Calcium (Ca^{2+}), magnesium (Mg^{2+}), and sulfur (SO_4^{2-}) are considered as secondary nutrients. Though essential, these are needed by plants in quantities less than the primary nutrients.

22.4.1 Calcium (Ca^{2+})

The Ca content of plants is 0.1–0.5%. A steady supply of 1–10 mM Ca^{2+} is required for normal plant growth (Gilroy et al. 1993).

Calcium (Ca^{2+}) is involved in regulating various fundamental processes such as cytoplasmic streaming, thigmotropism, gravitropism, cell division, cell elongation, cell differentiation, cell polarity, photomorphogenesis, plant defense, and stress responses. Cytoplasmic concentration of Ca^{2+} needs to be strictly regulated at nanomolar (nM) range (100–200 nM), though Ca^{2+} concentrations in μM to mM ranges are found in cell wall and plasma membrane externally and vacuole, endoplasmic reticulum, plastids, and mitochondria internally. It has been reported that both in flowering and nonflowering plants, cytoplasmic streaming is permitted at a low Ca^{2+}

concentration of 0.1 μM, but an elevated concentration of 1 μM inhibits the process (Hepler 2005).

22.4.1.1 Mechanism of Calcium Uptake and Homeostasis

Calcium homeostasis in cytoplasm is achieved through regulation of influx and efflux of Ca^{2+} ions by calcium channels.

Influx is carried out by (i) depolarization-activated cation channels (DACC), (ii) hyperpolarization-activated cation channels (HACC), and (iii) voltage-independent cation channels (VICC). There are also outward-rectifying cation (KORC or NORC) channels, mechanosensitive (stretch-activated) channels, and second messenger-activated Ca^{2+} channels.

Efflux of Ca^{2+} *from cytosol is carried out* by (i) Ca/H^+ antiporters, which mediate a high-affinity low turnover efflux, and (ii) P-type Ca-ATPases, which mediate a low-affinity high-capacity efflux of Ca^{2+}. Antiporters reduce signal-mediated influx of Ca^{2+} concentration by a few micromolar, whereas ATPases maintain the low resting concentration of Ca^{2+} (Hirschi et al. 1996). Ca^{2+} is present in mM concentration in vacuole, whereas its concentration in cytosol is in nanomolar range.

22.4.1.2 Calcium and Abiotic Stress

The abiotic stresses such as cold, heat, salinity, drought, osmotic and oxidative stresses, physical stimuli (touch and swaying of the plants by wind), etc. cause transient perturbations of cytosolic Ca^{2+} concentration, which are restored to basal levels within minutes. Mechanical stimuli, such as touch and bending, stimulate distinct pattern of Ca^{2+} response in the roots of *Arabidopsis.* There is monophasic elevation of cytosolic Ca^{2+} at the touch site, whereas bending involves biphasic elevation of cytosolic Ca^{2+} in the cells on the convex side of the roots. Transient perturbations of cytosolic Ca^{2+}concentrations also occur in response to hormones. All such changes are triggered by cellular second messengers such as NAADP, IP3, IP6, sphingosine-1-phosphate, and cADPR (Lemtiri-Chlieh et al. 2003; Kudla et al. 2010). The term "Ca^{2+} signature" is used to define the pattern of perturbation in cytosolic Ca^{2+} concentration in its intensity, amplitude, and duration caused by physiological, developmental, or environmental changes.

22.4.1.3 EF Hands and Ca^{2+} Sensing and Signaling

A large set of calcium-binding proteins in plants known as cellular Ca^{2+} sensors act as first information translation point (Kim et al. 2007; Kudla et al. 2010). These proteins have one or more highly conserved Ca^{2+} binding helix-turn-helix structures known as EF hands, which bind Ca^{2+} with high affinity (White 2003). Pairs of EF hands may interact through antiparallel β-sheets, which cooperatively bind Ca^{2+}. EF hand sensors are of two types. These include sensor relays such as calmodulins (CaMs), CaM-like proteins (CMLs), and calcineurin B-like proteins (CBLs) and sensor responders such as Ca^{2+}-dependent protein kinases (CDPKs), $Ca^{2+}$and Ca^{2+} CaM-dependent protein kinases (CCaMKs), some DNA, lipid-binding proteins, and a few enzymes (Harper and Harmon 2005; Reddy et al. 2011).

It is evident from several global studies that reprogramming of transcriptome is an important part of stress signaling and adaptation (Reddy et al. 2011). Perturbation in cellular or nuclear Ca^{2+} levels modulates gene expression (Kaplan et al. 2006; Reddy et al. 2011). Increase in levels of extracellular Ca^{2+} results in increase in expression of several genes including those involved in encoding Ca^{2+} sensors. Expression of some of the genes in response to heat or cold shock also depends on external Ca^{2+} concentration (Braam 1992; Polisensky and Braam 1996). Bioinformatic analysis of *Arabidopsis* genome indicates the presence of 230 Ca^{2+}-responsive genes, of which 162 are upregulated and 68 downregulated. A significant occurrence of two consensus ABRE (abscisic acid-responsive element) *cis*-elements (CACGTG[T/C/G]) and its coupling element ([C/A] ACGCG[T/C/G]) has been found (Kaplan et al. 2006). It has been observed from kinetic studies that Ca^{2+}-responsive genes reach their maximum expression within 30 min in response to a stimulus (Kaplan et al. 2006).

22.4.1.4 Abiotic Stress, miRNA, and Ca^{2+} Sensors

CDPK (calcium-dependent protein kinases), CIPK (CBL-interacting protein kinases), and EF-hand family of Ca^{2+} sensors could be regulated by NR030, miR399j, and miR1318/1432, respectively. Overexpression of CDPK probably occurs under drought stress. NR030, which is involved in regulating CDPK, is downregulated under conditions of drought stress. Overexpression of CDPK gene in rice, OsCDPK7, enhanced induction of some stress-responsive genes in response to salinity/drought, but not cold. CDPKs, which contain both calmodulin-like calcium binding and serine/threonine protein kinase domains, are only present in plants and some protozoans. Upon activation by a stimulus, they transduce the signal through phosphorylation cascades to induce downstream responses, including transcriptional regulation. miR1318/1432, which are downregulated under drought stress condition, can also regulate the EF-hand family proteins (Boudsocq and Sheen 2010; Bakhshi et al. 2016).

22.4.1.5 Ca^{2+}-Regulated Gene Expression in Response to Some Specific Abiotic Stress

Plants encounter various types of stress as they grow under different climatic conditions, soil types, and management practices and have to respond to each individually, sometimes superimposed on each other.

Drought It is reported that more than 95% of water translocated through plants exit through the stomatal pores, which are also involved in uptake of CO_2 for use in photosynthesis. Cytosolic Ca^{2+} regulates closure of stomata by two mechanisms:

(i) Short-term Ca^{2+}-reactive closure, rapid reactions induced by cytosolic Ca^{2+}, when it exceeds a threshold limit
(ii) Long-term Ca^{2+}-programmed closure, which involves prevention of stomatal reopening, controlled by specific Ca^{2+} signature, Ca^{2+}oscillation within a defined range of amplitude, frequency, duration, and overall transient number (Allen et al. 2001; Sanders et al. 2002; Kudla et al. 2010)

Exogenous Ca^{2+} has been reported to enhance drought resistance, inhibit synthesis of activating oxides, protect the structure of plasma membrane, maintain normal photosynthesis, and regulate the metabolism of plant hormones. Cellular Ca^{2+} as a second messenger transmits drought signal and induces physiological response to water stress (Zhang et al. 2001; Tuberosa et al. 2007; Song et al. 2008). Ca^{2+}/CaM messenger system is reported to be involved in controlling stress resistance of rice seedlings; blocking messenger transduction, drought resistance, and salt tolerance; and decreasing cold resistance (Zong et al. 2000). Treatment of rice seedlings with Ca^{2+} increases protection against membrane lipid peroxidation, stabilizes membranes, and increases their drought resistance (Lu et al. 1993).

Microarray analysis of *Arabidopsis* genome shows that several hundred genes are expressed in a specific pattern due to water deficiency in plants (Seki et al. 2002; Yamaguchi-Shinozaki and Shinozaki 2006, Reddy et al. 2011). Such expressions are induced by many Ca^{2+}-binding proteins (protein kinases/phosphatases) and TFs (AREBs and DREBs), chaperones, and molecules involved in osmoprotectant metabolism (Reddy et al. 2011).

The synthesis of phytohormone ABA is induced under water stress conditions. The increased levels of ABA signal closure of guard cells and induce expression of drought stress-related genes. These genes encode proteins, which provide dehydration tolerance to plants (Reddy et al. 2011). ABA may regulate ABA-responsive genes through cellular Ca^{2+} changes (Kaplan et al. 2006). It is reported that in the presence of Ca^{2+}, the overexpression of TaTPC1 (which functions for Ca^{2+} import in wheat cytosol) accelerates stomatal closing (Wang et al. 2005).

Cold Ca^{2+}-permeable channel proteins have been reported to be primary temperature sensors in plants and are involved in plant response to cold stress (Pleith et al. 1999). It has been observed in alfalfa, barley, and *Arabidopsis* that Ca^{2+} influx acts as signal transduction element for gene expression at low temperature (Plieth et al. 1999; Busconi et al. 2001). Cold acclimation by temperate plants involves changes in gene expression (Fowler and Thomashow 2002; Kreps et al. 2002, Reddy et al. 2011). A large number of genes of CBF regulon are induced during the process of cold acclimation. These genes are activated by transcription factors, C-repeat binding factors, and CBF1, 2, and 3 also called DREB1B, 1C, and 1A, respectively

(Reichmann et al. 2000; Maruyama et al. 2004; Sakamoto et al. 2004; Vogel et al. 2005, Reddy et al. 2011). The induction of KIN1 a member of CBF regulon due to cold requires a rapid increase of cytosolic Ca^{2+} (Monroy et al. 1997). A number of cold-responsive genes contain CAMTA (calmodulin-binding transcription factor) binding sequence CGCG and may be regulated transcriptionally by CAMTA proteins on exposure to cold (Doherty et al. 2009).

Heat Heat-shock proteins (HSPs) are synthesized by plants in response to higher temperature. Their transcription is tightly regulated by TFs. Among the five conserved families of HSPs (HSP100, HSP90, HSP70, HSP60, and sHSP), only small HSPs (sHSPs) are prevalent in plants. sHSPs vary in size from 12 to 40 kDa (Vierling 1991; Lewis et al. 1999). Overexpression of a CaM-binding phosphatase (PP7) in *Arabidopsis* has been found to increase expression of heat-shock proteins and provide thermotolerance. A CaM-binding protein kinase (CBK) in *Arabidopsis* phosphorylates heat-shock TF (AtHSFA1a) and regulates transcription of HSPs, which provide thermotolerance (Liu et al. 2007). CAMTA1 is also involved in heat-shock response (Galon et al. 2010).

Salt A large number of genes are activated on exposure to salinity, including ion channels, receptors, signaling molecules, and genes involved in producing compatible molecules such as osmoprotectants, glycine betaine, and proline (Tuteja 2007; Reddy et al. 2011). The salt stress-mediated Ca^{2+} signatures are decoded by “salt overly sensitive” (SOS) pathway. Under saline conditions SOS1, a plasma membrane-localized Na^+/H^+ antiporter, exports Na^+ to the apoplast. The SOS3 (CBL4)/SOS2(CIPK24) complex modulates the expression of SOS1 and regulates ion homeostasis (Chinnusamy et al. 2004; Mahajan et al. 2008; Reddy et al. 2011; Jia et al. 2013).

Saline stress and other abiotic and biotic stress upregulate a number of CAMTA family TFs (Galon et al. 2010). Salt-induced Ca^{2+} signaling has also been found to activate MYB2 TF, which is an upstream regulator of a number of salt- and dehydration-responsive genes (Yoo et al. 2005). A soybean CaM isoform induced by salt stress is Gm-CaM4. Overexpression of Gm-CaM4 induces constitutive expression of salt- and dehydration-responsive genes, including proline-synthesizing enzyme P5CS1 (Δ-1-pyrroline-5-carboxylate synthetase-1), which facilitates proline accumulation and provides protection against salt stress (Yoo et al. 2005).

Mechanical Stimuli Different types of mechanical stimuli induce distinct type of Ca^{2+} response in *Arabidopsis* roots. Touch stimuli induce monophasic elevation of cytosolic Ca^{2+} concentration at the touch site. Bending induces biphasic transient elevation of cytosolic Ca^{2+} concentration on the convex (stretching) side. Such responses are essential for the apoplastic alkalization and RBOH C-dependent apoplastic ROS production that may contribute to plant resistance to stress (Monshausen et al. 2009).

Mechanical stimuli induce expression of several CaM and CaM-related genes (Braam 2005; van Der Luit et al. 1999; Walley and Dehesh 2010; Reddy et al. 2011). Mechanical stress-induced transcriptomic study and bioinformatic analysis of data identified an overrepresented cis-element "CGCGTT" termed as rapid stress response element (RSRE) in the promoter region of rapid wound-responsive genes (Walley et al. 2007). This cis-element contains the CAMT core cis-element "CGCG." This indicates that CAMTAs are probably involved in stress response to wounding (Walley et al. 2007; Walley and Dehesh 2010; Reddy et al. 2011).

22.4.2 Magnesium (Mg^{2+})

Mg^{2+} concentration in crops varies from 0.1% to 0.4%. The critical limit of Mg^{2+} in dry banana leaves has been reported to be 0.3% and of coconut 0.2% (14th fond) (Mitra 2006). The free Mg^{2+} level in the cytosol is strictly regulated due to its role in photosynthesis and on membrane ionic currents (Shaul 2002). The concentration of Mg^{2+} in the metabolic pool of leaf cells (cytoplasm and chloroplast) is reported to be 2–10 mM (Leigh and Wyn Jones 1986). Free Mg^{2+} concentration is considerably less. About 90% of Mg^{2+} is complexed with cytoplasmic ATP. Vacuole is the main organelle, which is involved in Mg^{2+} homeostasis in the cytosol and chloroplast (Marschner 1995).

Mg^{2+} deficiency affects root growth of the plants and hence nutrient and water uptake (Marschner 1995). Mg^{2+} is also involved in Ca^{2+}-based signal transduction processes (Baumann et al. 1991). Mg^{2+} deprivation elicits rapid Ca^{2+} uptake and activates Ca^{2+}/calcineurin signaling (Wiesenberger et al. 2007). Low magnesium concentrations may become a limiting factor for functional intracellular communication (Geberta et al. 2009). Mg^{2+} acts as cofactor of many enzymes, such as RNA polymerase, ATPases, protein kinases, phosphatases, carboxylases, and glutathione synthetase. It is required for aggregation of ribosomes and is the central atom of chlorophyll molecule. Small variation in Mg^{2+} level in the cytosol and chloroplast strongly affects key photosynthetic enzymes (Shaul 2002). During the process of chlorophyll formation, insertion of Mg^{2+} into the porphyrin structure is catalyzed by Mg^{2+} chelatase (Walker and Weinstein 1991; Papenbrock et al. 2000). Chlorophyll breakdown is caused by Mg^{2}-dechelatase with the formation of pheophytin (Langmeier et al. 1993).

22.4.2.1 Mechanisms of Mg^{2+} Uptake and Homeostasis in Plants

Mg^{2+} is unique among the biologically active divalent cations with the smallest ionic radius, highest charge density, and largest hydrated radius. Mg^{2+} often interacts with other molecules maintaining its hydration sphere. There is a 400-fold difference between volumes of hydrated and non-hydrated states (Li et al. 2001; Geberta et al. 2009).

The proteins involved in transport of Mg^{2+} across biological membranes have unique structures (Moomaw and Maguire 2008; Geberta et al. 2009). The mechanism of Mg^{2+} transport involves the binding of the fully hydrated cation to an extracellular binding loop, which connects the TM domains. No electrostatic interactions are involved in passage of the cation through the membrane. The gene of bacterial membrane transport proteins for Mg^{2+}, *CorA*, appears to be a constitutive gene since it is not transcriptionally regulated. CorA homolog proteins have been found in all living organisms including plants. *Arabidopsis* has ten members of this gene family. Initially named as AtMRS2 and subsequently AtMGT, they constitute Mg^{2+} transporter of higher plants as well (Li et al. 2001). There are nine Mg^{2+} transporter proteins encoded by rice genome, which are homologs of *AtMRS2/MGT* gene family.

ZmPIP1;5 aquaporin genes present in maize leaf exhibit the same expression pattern as magnesium transporter CorA-like family proteins and may be involved in metal ion transmembrane transporter activity in the developing leaf (Yue et al. 2012).

22.4.2.2 Mg^{2+} and Heavy Metal Stress

Mg^{2+} substitution in vivo in the chlorophyll by heavy metals (Hg^{2+}, Cu^{2+}, Cd^{2+}, Ni^{2+}, Zn^{2+}, Pb^{2+}) under conditions of heavy metal stress impairs photosynthesis (Kupper et al. 1996, 1998). Mg^{2+} is involved in both light and dark reactions of photosynthesis. Mg^{2+}-deficient leaves are therefore highly photosensitive (Shaul 2002).

22.4.2.3 miRNA, Mg Deficiency, and Stress-Related Genes

Limited data are available on Mg deficiency and expression of miRNA. Ma et al. (2016) isolated 73 known and 2 new miRNAs which were upregulated and 64 known and 7 new miRNAs which were downregulated due to Mg deficiency in the leaves of *Citrus sinensis*. According to them:

(i) Downregulation of miRNAs, "*miR164*, *miR7812*, *miR5742*, *miR3946*, and *miR5158*," upregulated stress-related genes.
(ii) Decreased expression of *miR3946 and miR5158* and increased expression of *miR*395, *miR*1077, *miR*1160, and *miR*8019 enhanced cell transport.
(iii) Repression of *miR158*, *miR5256*, and *miR3946* activated lipid metabolism-related genes.
(iv) Repressing *miR779* induced cell wall-related gene *expansin 8A*.
(v) Upregulating *miR395 and miR6426* and upregulated expression of genes involved in homeostasis of S, K, and Cu.

They also identified some candidate miRNAs that might contribute to Mg deficiency tolerance of *C. sinensis* plants.

22.4.2.4 Role of Mg^{2+} in Alleviation of Al^{3+} Toxicity

It has been observed that grasses and cereals treated with Al^{3+} show Mg^{2+} deficiency (Tan et al. 1991) and application of higher levels of Mg^{2+} can alleviate Al^{3+} toxicity (Tan et al. 1991; Matsumoto 2000). It has also been shown that Al^{3+} inhibits Mg^{2+} uptake by roots (Rengel and Robinson 1989). The hydrated radius of Mg^{2+} and Al^{3+} is similar (Bose et al. 2011). At millimolar concentration Mg^{2+} can effectively compete with Al^{3+} for the same binding sites of the roots. Enhanced excretion of organic acids is also a likely mechanism in Mg^{2+}-mediated alleviation of Al^{3+} toxicity.

Rice is the most Al^{3+}-tolerant crop among the cereals. This is due to the presence of multiple Al tolerance genes involved in detoxification of Al^{3+} at different cellular levels regulated by a transcription factor ART1 (Al^{3+} resistance transcription factor 1) (Tsutsui et al. 2011). ART1 is a Cys2-His2 type Zn-finger TF and is constitutively expressed in roots (Yamaji et al. 2009). ART1 regulates expression of 31 genes downstream through a cis-acting element, GGN (T/g/a/C)V(C/A/g)S(C/G). This element was found in the promoter region of 29 genes out of 31 ART1-regulated genes (Tsutsui et al. 2011).

22.4.3 Sulfur

Sulfur (S) is an essential plant nutrient and is considered as the fourth major nutrient after N, P, and K (TSI 2008). It is also of importance in human and animal nutrition. The total S content of plant tissues has been reported to be 0.5–1.5% of the dry weight of the plants (Zhao et al. 1993; Marschner 1995; Burandt et al. 2001). Sulfur is a constituent of various organic plant constituents. Sulfur is a constituent of amino acids cysteine and methionine, which are involved in maintaining protein structure and conformation. It is a constituent of coenzymes and prosthetic groups such as lipoic acid, coenzyme A, thiamine, etc. Sulfur compounds are involved in response to abiotic and biotic stress, such as glutathione in the detoxification of active oxygen species. Sulfur plays an important ecological role in defense against herbivores and pathogens.

22.4.3.1 Effects of S Deficiency on Yield and Quality of Crops

Field experiments at Rothamsted show that yield loss due to S deficiency in oilseed rape can be up to 70% and in cereals up to 50% (Zhao et al. 2001). Oilseed crops generally have a higher requirement of S as compared to other crops. S deficiency also affects quality of crops. Under limiting S availability, wheat grains accumulate low sulfate storage proteins such as ω-gliadin and high molecular weight subunits of glutenin at the expense of S-rich proteins. Such changes in protein composition affect dough rheology. Bread-making quality of wheat is closely correlated with S content of grain rather than N content (Zhao et al. 1999). Adequate S supply has been reported to increase both yield and malting quality of barley. S application significantly increases concentration of S-methyl methionine (the precursor of dimethyl sulfide) in kilned malt, which affects beer flavor (Zhao et al. 2006). The oil content of oilseeds is reported to increase due to S application as follows: sunflower, 3.8%; linseed, 6%; soybean, 9.2%; mustard, 9.2%; and groundnut, 11.3%. Quality of tea has been reported to improve due to S application (TSI 2008). There are positive effects of sulfur application on morphine, codeine, and thebaine content of opium (Subrahmanyam et al. 1992). Plant glucosinolate content of Brassicales has been reported to increase from 25% to more than 50-fold depending upon the plant species, amount of S fertilizer used, and type of treatment (Falk et al. 2007).

22.4.3.2 Sulfur Uptake and Homeostasis in Plants

Sulfate (SO_4^{2-}) is the major form of inorganic S taken up directly from soil and transported in xylem (Falk et al. 2007). The cytoplasmic concentration of sulfate remains more or less constant. The excess sulfate is stored in the vacuole. In general shoot growth is more significantly affected than root growth in response to S availability (Marschner 1995). Under prolonged S deprivation, the partitioning of S between shoot and root is in favor of root growth (Buchner et al. 2004).

22.4.3.3 Pathway for Assimilation of Sulfur in Plants

Sulfate is first acted upon by ATP sulfurylase (ATPS) to form adenosine-5′-phosphosulfate (APS). APS is reduced by APS-reductase to sulfite in plastids of plants. It is further reduced to sulfide by sulfite reductase (SiR). Sulfide is then catalyzed by OAS (thiol) lyase (OALS) and incorporated into amino acid skeleton of O-acetyl serine (OAS) to form cysteine (see Fig. 22.2).

22.4.3.4 Mechanism of Sulfate Transport in Plants

Plasma membrane sulfate transport is probably a pH-dependent proton-coupled cotransport involving $3H^+/SO_4^{2-}$ stoichiometry. The sulfate transporter protein expressed in the plasma membrane of root cells consists of a single polypeptide chain of around 70–74 kD. A large number of sulfate transporter genes have been identified from *Arabidopsis*, rice, and other plants. In *Arabidopsis*, the gene family consists of 14 isoforms, which can be subdivided into 5 groups. Wheat, *Brassica oleracea*, and rice have similar gene groups and are close homologs with similar functions. Group I high-affinity transporters are located in the plasma membrane. Group II low-affinity transporters are also located in the plasma membrane. Group III, of unknown function, may be associated with hetero-dimer association (Kataoka et al. 2004a). Group IV are involved in efflux of sulfate across tonoplast of vacuole into cytoplasm (Kataoka et al. 2004b). A member of group V, Sultr 5;2, is probably

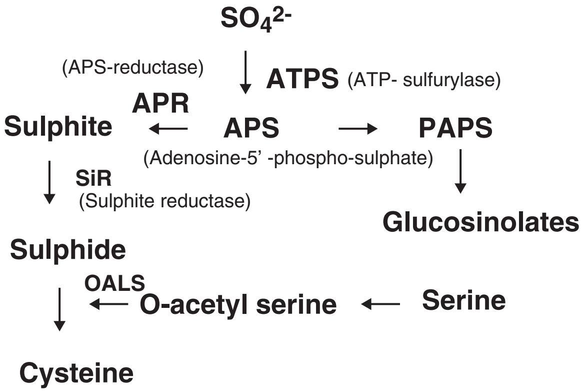


Fig. 22.2 Assimilation of sulfate into organic compounds

an intracellular transporter involved in Mo metabolism in *Arabidopsis* and named as MOT1 (Baxter et al. 2008). Mo and Se are probably taken up through sulfate uptake pathway (Shinmachi et al. 2010).

22.4.3.5 N Deficiency and Regulation of SO_4^{2-} Uptake

S uptake is closely coordinated with N and C metabolism. There is an induction of the genes of high-affinity sulfate transporters due to addition of sucrose. Nitrogen deficiency strongly reduces sulfur uptake, consequently a significant reduction in accumulation of transcripts of high-affinity sulfate transporters AtSultr1;1 and AtSultr1;2 (Maruyama-Nakashita et al. 2004). However, S deficiency does not decrease total N content, although there is an increase in O-acetyl serine (OAS), which is the precursor for synthesis of cysteine and has a role in regulation of sulfate uptake and reduction (Hawkesford 2000).

The promoter region of *AtSultr1;1* has been found to contain a 16 bp sulfur-responsive element (SURE), which includes an auxin-responsive factor (ARF) binding sequence (GAGACA). ARF-binding site has a 5 bp core element (GAGAC), which regulates expression of a set of genes required for adaptation of plants to sulfur-deprived conditions. A transcriptional regulator sulfur limitation1 (SLIM1) has been reported to upregulate *AtSultr1;1*, *AtSultr1;2,* and *AtSultr4;1* gene expression in response to S deprivation in *Arabidopsis.*

22.4.3.6 Regulation of Sulfate Uptake Genes Under Abiotic Stress

Generally, there is reduced uptake of nutrients under salt- and water-stressed conditions. Several *Sultr* genes re-equilibrate sulfate flux in the aerial parts of the plants under abiotic stress. Drought causes significant reduction in expression *Sultr2;1* in leaves of *A. thaliana* and *M. truncatula* and causes decreased flux of sulfate to younger leaves, a mechanism probably to save sulfate (Gallardo et al. 2014).

22.4.3.7 Role of Sulfur-Rich Compounds on Alleviation of Heavy Metal Stress

Phytochelatins (PCs) and metallothioneins (MTs) are two cysteine-rich metal-binding polypeptides found across most of the taxonomic groups (Hall 2002; Grennan 2011).

Phytochelatins (PCs) have general structure (γ Glu-Cys)$_{n}$ - Gly, where $n = 2–11$. The genes of PCs occur in a large number of plants, and the enzyme, phytochelatin synthase (PCS), is constitutively expressed. PCs are synthesized non-translationally from glutathione (GSH) as a substrate by phytochelatin synthase (PCS), an enzyme that is activated in the presence of metal ions. PCs are involved in major detoxification mechanisms. PC-metal complexes have been detected in plant cells with Cd, Ag, Cu, and As.

Metallothioneins (MTs), similar to phytochelatins (PCs), are cysteine-rich but are gene-encoded polypeptides. Plant MTs (including *Arabidopsis*) show large sequence diversity and have been classified into four subfamilies (MT1, MT2, MT3, and MT4) based on the arrangements of Cys residues. Wheat E proteins isolated from wheat germ bind Zn^{2+} at a stoichiometry (Zn^{2+}/protein) of approximately 5:1 and are classified as class II metallothioneins. Apart from metal binding (Zn, Cd, and Cu), MTs have been reported to play a role in other cellular processes such as regulation of cell growth and proliferation, DNA damage repair, scavenging of ROS, and a Zn donating role.

22.4.3.8 miRNA and S Homeostasis

Expression of miR395 is significantly upregulated during S deficiency. Genes of two families involved in sulfate metabolism are targeted by miR395: (i) the APS genes coding ATP sulfurylase isoforms, ATPS1, ATPS3, and ATPS4, and (ii) the genes of low-affinity sulfate transporters, Sultr2;1, which are located in the xylem parenchyma cells of roots and shoots. Sultr2;1 is cleaved by miR395 (Liang et al. 2010). Distribution of S is impaired from older to younger leaves in miR395 overexpressing plants (Liang et al. 2010). According to Kawashima et al. (2009), miR395 loci are expressed in the vascular system of leaves, roots, and root tips under S-deficient conditions. Translocation of miR395 from leaves to roots through phloem is not necessary under S-deficient conditions. Induction of miR395 is controlled by the transcription factor SLIM1 involved in S-assimilation pathway (Kawashima et al. 2009).

22.4.4 *Micronutrients*

Micronutrients are required in smaller quantities as compared to primary and secondary nutrients but are essential for plant nutrition. When their concentration in the growth medium is below a critical limit, plants show characteristic deficiency symptoms. Heavy metals, which do not have micronutrient functions, do not show such deficiency symptoms. Micronutrients some of which are considered also as heavy metals do show toxicity symptoms beyond a critical concentration. Currently micronutrients include Zn, Fe, Mn, Cu, B, Mo, Co, and Ni.

22.4.5 *Zinc (Zn^{2+})*

Zinc (Zn^{2+}) is a micronutrient essential for plant growth. Zn concentration in plants is within a range of 25–150 μg g^{-1}. Zinc concentration less than 15–20 μg in leaves per gram of dry leaf tissues leads to Zn deficiency.

22.4.5.1 Zn Stress due to Deficiency and Toxicity

In plants, Zn deficiency syndromes include chlorotic leaves, early senescence, and stunted growth. Toxic symptoms of Zn generally appear in younger leaves as chlorotic spots, which progress to reddening of leaves due to increased anthocyanin synthesis.

Plants take up Zn as a divalent cation (Zn^{2+}). Inside the plant cell, it is neither oxidized nor reduced, but has a strong tendency to form tetrahedral complexes (Berg and Shi 1996; Schützendübel and Polle 2002). Zn becomes toxic at higher concentrations, which vary for different plants and the parts of plant such as leaves, shoots, and roots. Toxic symptoms generally appear in younger leaves as chlorotic spots, which progress to reddening of leaves due to increased anthocyanin synthesis. Zn toxicity also results in smaller leaves and reduced root growth (Fontes and Cox 1995; Reichman 2002).

22.4.5.2 Mechanisms of Zn^{2+} Uptake and Homeostasis and Interaction with Cd

It is essential to maintain Zn^{2+} homeostasis within various organs of plants at an acceptable physiological limit. This is carried out by a coordinated expression of Zn^{2+} transporters, which are involved in Zn^{2+} uptake from the soil, translocation of Zn^{2+} to various organs and tissues, in intracellular sequestration and transport to vacuole.

The Heavy Metal Transporters (HMAs) belong to P_{1B} subfamily of P-type ATPase superfamily. The Zn cluster transporters transport divalent cations including Zn^{2+}. AtHMA2 of *Arabidopsis* drives efflux of Zn^{2+} from the plant cell and controls concentration of nonphysiological heavy metals such as Cd^{2+}. HMA2 and HMA4 play a key role in transport of Zn^{2+} from cell to cell and in transport of Zn^{2+} from root to shoot. HMA4 is the main Zn^{2+} transporter in *A. thaliana* and *A. halleri*. In barley HvHMA2, with a conserved aspartate phosphorylating site, functions as a Zn^{2+}/Cd^{2+} pump (Mills et al. 2012).

Plant Cadmium Resistance (PCRs) Transporters *Arabidopsis* PCRs, which provide Cd^{2+} resistance to plants, constitute a small gene family with 12 members and code proteins that differ in their N-terminal domains. They are subdivided into three clades: the first clade includes only PCR10, the second clade consists of seven members (not characterized), and the third clade consists of PCR1, PCR2, PCR3, and PCR11. PCR1 is strongly expressed in leaves and PCR2 in roots and leaves. PCR2 performs two independent functions: (i) it is involved in loading Zn^{2+} into the xylem and (ii) detoxification of excess Zn^{2+} at the root epidermal cells.

The MTPs (Metal Transporter Proteins) The MTPs are highly specific for Zn^{2+}. In *Arabidopsis* AtMTP3, which is localized in the vacuole of the epidermal cells of roots, controls Zn^{2+} partitioning and provides basic cellular Zn tolerance under conditions of high rates of influx of Zn^{2+} into the root symplasm (Arrivault et al. 2006).

The ZIP (ZRT- and IRT-Like Proteins) Family There are 15 ZIP genes in *Arabidopsis* (Maser et al. 2001). Recent report from yeast complementation studies (Milner et al. 2013) suggest that, possibly, ZIP7 can transport Zn, Mn, and Fe; ZIP1 and ZIP2 transport Zn and Mn; ZIP3, ZIP11 and ZIP12 transport Zn alone; ZIP5, ZIP6, and ZIP9 transport Mn alone; and none can transport Cu. According to them (Milner et al. 2013), AtZIP1 does not have a major role in Zn uptake. OsZIP4 in rice is localized in apical cells and is involved in Zn uptake.

Mugineic Acid Zn deficiency in barley plants is reported to induce synthesis and secretion of mugineic acids, which are effective in Zn uptake from the soil (Suzuki et al. 2006). Deoxymugineic acids translocate and distribute Zn^{2+} within the rice shoot under Zn-deficient conditions but not involved in Zn^{2+} uptake (Suzuki et al. 2008).

22.4.5.2.1 Transcription Factors (TFs)

TFs have been reported to be involved in molecular control of Zn^{2+} homeostasis in plants under Zn^{2+} deficiency. Two members of *bZIPs TF* gene families, *bZIP19* and *bZIP23*, isolated from *Arabidopsis* are possibly involved in transcriptional regulation for adaptation to Zn deficiency. The bZIP19 and bZIP23 proteins bind to a palindromic 10 bp *ZDRE (zinc deficiency response element, RTG TCG ACA Y)*, which is unique to plant, in the upstream region of 8 out of a group of 15 ZIP family of cation transporters. The functions of bZIP19 and bZIP23 are essential for a proper Zn^{2+} deficiency response and allow *Arabidopsis* to grow under Zn deficiency. Such Zn homeostasis mechanism possibly operates in all plants under Zn^{2+}-limiting conditions (Assunção et al. 2010).

22.4.5.3 Abiotic Stress, miRNA, and Zn^{2+} Homeostasis

Most biotic and abiotic stresses including those due to heavy metals cause production of reactive oxygen species (ROS). Expressions of two closely related Cu/Zn superoxide dismutase (cytosolic CSD1 and chloroplastic CSD2) transcripts (which can detoxify oxidative stress) are induced in response to oxidative stress. Oxidative stress also downregulates transcription of miR398, which otherwise would have cleaved mRNA of CSD1 and CSD2. This results in posttranscriptional accumulation of mRNA of CSD1 and CSD2 (Sunkar et al. 2006).

Oxidative stress caused by Fe and Zn toxicity also causes downregulation of expression of miR398 and upregulation of CSDs. The genes of *miR398a, miR398b,* and *miR398c* are differently expressed in leaves and roots of *Arabidopsis* due to Zn toxicity. Transcription of *miR398a* decreases in leaves and roots, but transcription of *miR398b* and *miR398c* is induced in leaves with no response in roots due to Zn abundance (Remans et al. 2012). Dong-qing et al. (2013) observed that out of 15 differentially expressed miRNAs, 13 were upregulated due to Zn deficiency stress in *B. juncea* roots and only 2 miR399b and miR845a were downregulated.

22.4.6 Iron (Fe^{3+})

Iron in soil is present in the form of an amorphous Fe $(OH)_3$ precipitate, which is the immediate source of iron uptake by plants. Availability of Fe to plant roots depends on redox potential and pH of the soil.

$$\mathrm{Fe}\left(\mathrm{OH}\right)_3 + 3\mathrm{H}^+ \rightleftarrows \mathrm{Fe}^{3+} + 3\mathrm{H}_2\mathrm{O}$$

Plant tissue concentration of 1–5 μM Fe is considered sufficient and a concentration below 1 μM is likely to cause deficiency. A concentration above 10 μM may cause toxicity with reduction of growth parameters (Mitra et al. 2009). However, these limits may vary considerably among different plant species and their genotypes.

22.4.6.1 Mechanism of Iron Uptake and Homeostasis in Plants

There are two distinct iron uptake systems based on the response of plants to Fe deficiency, strategy I and strategy II.

Strategy I Plants These include all dicots and non-*graminaceous* monocots. Fe deficiency causes a decrease in rhizosphere pH of these plants to facilitate release of Fe^{3+} ion from insoluble sources. The sparingly soluble ferric iron is then reduced at the root surface by membrane-resident NADPH-dependent ferric chelate reductase. Reduced ferrous iron is absorbed into root cells by the high-affinity Fe^{2+} transporter, IRT1 (iron-regulated transporter 1), a member of the ZIP metal transporter family. IRT1-likeFe^{2+} transporters have been isolated from several dicotyledonous species. All the three components of Fe uptake by strategy I plants, such as (i) release of protons to lower pH, (ii) expression of ferric chelate reductase gene to augment enzyme activity, and (iii) expression of IRT1 transporter for absorption of Fe by root cells, increase substantially when plants are grown under Fe-deficient conditions. Reduced ferrous iron is absorbed into root cells by the high-affinity Fe^{2+} transporter, IRT1, a member of the ZIP metal transporter family. IRT1-like Fe^{2+} transporters have been isolated from several dicotyledonous species.

Strategy II Plants These are limited to *graminaceous* monocots. These plants release mugineic acid family phytosiderophores (MAs) to the rhizosphere, where they solubilize sparingly soluble iron by chelation. The chelated complex is then absorbed into the roots. Rice plants use MAs to acquire Fe from the rhizosphere. The synthesis of MAs proceeds throughout the day and is stored in the roots (as much as 1–2% of root dry weight) and secreted to the rhizosphere next morning (Ma et al. 1995). Synthesis of MAs and uptake of MA-chelated iron are strongly induced under iron-deficient conditions. It has been reported that all the Fe deficiency-induced genes involved in Fe uptake have a higher incidence of homologous sequences of *IDE1* and *IDE2* (iron deficiency-responsive *cis*-acting elements) in their promoter regions (Kobayashi et al. 2005).

Iron Transporters The transporters involved in Fe uptake are:

(i) ZIP (ZRT IRT-like proteins) family (AtIRT1, AtIRT2; OsIRT1, OsIRT2, etc.) involved in high-affinity iron transport (Connolly et al. 2002).
(ii) ABC (ATP-binding cassette) transporter: AtABCB25 (AtATM3) is a mitochondrial ABC transporter involved in biogenesis Fe-S clusters in plants (Kushnir et al. 2001; Bernard et al. 2009).
(iii) Nramps (*natural resistance-associated macrophage proteins*) (AtNramp1, AtNramp3, AtNramp4, OsNramp5, LeNramp1, AhNramp1, etc., found in various plants) involved in Fe transport (Lanquar et al. 2005; Ishimaru et al. 2012; Mitra 2015).
(iv) H^+-ATPase (expressed in the root epidermis) releases protons to the rhizosphere, which lowers pH and makes iron more soluble. Fe deficiency upregu-

lates the H^+-ATPases, AHA1, AHA2, and AHA7, in the root epidermis (Morrissey and Guerinot 2009).

(v) The YSL (yellow stripe-like) transporter. YS1 found in Poaceae roots is a proton-coupled symporter of Fe(III)-PS complexes (Schaaf et al. 2004).

22.4.6.2 Iron Homeostasis in Subcellular Organelles

Chloroplasts and Mitochondria Up to 90% of Fe in leaves is associated with lipoproteins of membranes of chloroplast and mitochondria. About 50% of Fe in chloroplast is located in the stroma and 50% in the thylakoid membranes. Iron is required as a cofactor in photosynthetic electron transport chain, biosynthesis of heme, and Fe-S cluster formation in the chloroplast. Chloroplasts store iron as ferritin and contain specific iron, chloroplasts store iron as ferritin and contain specific iron transporter proteins such as YSL4 andYSL6 transporters (Divol et al. 2013) and PIC1 (permease chloroplast1), which remove Fe and do not allow Fe to accumulate in toxic concentrations (Duy et al. 2007).

Fe Homeostasis in Vacuole Vacuole is an initial source of Fe for germinating seeds. VIT1 (vacuolar iron transporter1) is an Fe-Mn transporter located in the vacuole and transports these metals into the vacuole. Loading of Fe through VIT1 and its proper distribution in the embryo is essential for seedling viability under low Fe conditions (Kim et al. 2006; Morrissey et al. 2009).

22.4.6.3 Fe Homeostasis and miRNA

Fe deficiency downregulates expression of miR397, miR398a, miR398b, miR398c, miR399, miR408, and miR2111, in contrast to upregulation of expression of these miRNAs due to Cu deficiency (see discussion under Cu homeostasis). Kong and Yang (2010) reported that 24 miRNA genes, which were upregulated due to Fe deficiency, had IED-1 and IED-2 (iron deficiency-responsive cis-acting elements) motifs in their promoter regions in *Arabidopsis*. Transcriptional analysis using RT-PCR showed that 70.8% (17/24) of the IED-containing miRNA genes were expressed in response to Fe deficiency.

22.4.7 Copper (Cu^{2+})

Copper deficiency is rarely observed in plants though it is an essential plant nutrient. Copper concentration in plant tissues is about 1–5 μg g^{-1} of dry weight (Marschner 1995) and in leaves 5–20 μg g^{-1} of dry weight (Baker and Senef 1995). However, there is considerable variation among plant species and their varieties.

Toxicity of Cu is observed beyond a threshold value, which differs among different species of plants and their genotypes. Threshold values have been reported for groundnut (shoot), 230 mg kg^{-1} (Borkert et al. 1998); soybean (shoot), 140 mg kg^{-1} (Borkert et al. 1998); rice (whole plant), 35 mg kg^{-1} (Borkert et al. 1998); rice (shoot), <20 mg kg^{-1}; wheat (shoot), 75 mg kg^{-1} (Wheeler and Power 1995); and black gram (leaves), 67 mg kg^{-1} (Kalyanaraman and Sivagurunathan 1993).

22.4.7.1 Mechanism of Cu Uptake and Homeostasis in Plants

Copper exists as Cu^{+} and Cu^{2+} forms under physiological conditions. The Cu^{+} form is preferably bound to the S in cysteine or methionine and Cu^{2+} form to N in histidine. Both deficiency and toxicity of Cu adversely affects crucial physiological processes in plants. Redox reactions between $Cu^{2+}$and Cu^{+} can catalyze production of highly toxic hydroxyl radicals (HO´), which fragment Cu/Zn SOD (Casano et al. 1997) and cause damage to cell membranes, nucleic acids, proteins, and other biomolecules (Halliwell and Gutteridge 1984). Deficiency of Cu reduces plastocyanin biosynthesis, which affects PSI electron transport (Shikanai et al. 2003). Cu-deficient chloroplasts have decreased PSII activity due to disintegration of thylakoid membranes and modification of PSII acceptor site (Heneriques 1989; Droppa et al. 1987). Several enzymes need Cu ion as a cofactor such as polyphenol oxidases, ascorbate oxidase, diamine oxidases, and laccase.

It is essential that Cu concentrations in tissues and cells need to be controlled within a narrow physiological range. This involves uptake of Cu from soil, transport to different parts of the plants, and regulation of its concentration in tissues, cells, and intracellular organelles. A wide range of gene families and proteins have been identified, which are involved in Cu homeostasis. Cu deficiency upregulates several *Arabidopsis* genes such as genes of COPT1 and COPT2, ZIP2 transporters, FRO3-metal reductases, CCH chaperones, and chloroplastic Fe-SODs (Himelblau et al. 1998; Sancenon et al. 2003; Abdel-Ghany et al. 2005; Mukherjee et al. 2006).

The *Arabidopsis* genome contains six genes encoding COPT transporters from COPT1 to COPT6. The well-characterized COPT1 is a high-affinity transporter specific for Cu^{+} ion. COPT1 transporters, possibly located in the plasma membrane, allow transport of Cu from exterior into cytoplasm. Their transport ability is stimulated by extracellular K^{+} ion. The *COPT1* gene is highly expressed in the root tips, stomata, embryos, trichomes, and pollen, and its expression is negatively regulated by Cu (Sancenon et al. 2003; Yruela. 2009).

AtHMA6/PAA1 (P_{1B} type ATPase of *Arabidopsis*1) transports Cu^{2+} in chloroplast and delivers cofactor to stomatal Cu/Zn superoxide dismutase. AtHMA8/PAA2 transports Cu into the thylakoid lumen to supply plastocyanin. AtHMA5 is involved in transmembrane transport of Cu and also interacts with Cu metallochaperones (CCH) (Andres-Colas et al. 2006). AtHMA7/RAN1 is associated with the delivery of Cu ions to ethylene receptors. HMA1 and PAA1 also form a distinct pathway for Cu import into chloroplast. There appears to be another alternate unidentified route for Cu import into chloroplast (Boutigny et al. 2014).

A family of nine proteins belonging to P_{1B}-type ATPases has been identified in rice and ten in barley (Williams and Mills 2005). In rice OsHMA1 to OsHMA3 belong to Zn cluster and OsHMA4 to OsHMA9 belong to Cu cluster.

CCH (Copper Chaperones) Copper chaperones belong to a family of metal receptors, which are cytosolic, soluble, and low molecular weight proteins involved in inserting Cu into the active sites of Cu-dependent enzymes (O'Halloran and Culotta 2000; Huffman and O'Halloran 2001). CCH protects highly active Cu^+ inside the cell from improper interactions with other cellular constituents (Hall and Williams 2003; Yruela 2009). It is involved in symplastic Cu transport through plasmodesmata associated with nutrient mobilization in senescing leaves (Yruela 2009).

CCS (Copper Chaperone for Cu/Zn Superoxide Dismutase) *CCS* (copper chaperone for Cu/Zn superoxide dismutase) genes (homologous to yeast *Ccs1p/Lys7p*) encode proteins, which deliver Cu to Cu/Zn SOD by a protein-protein interaction.

22.4.7.2 miRNA and Regulation of Abiotic Stress due to Cu

Cu sufficiency upregulates expressions of two closely related Cu/Zn superoxide dismutase (cytosolic CSD1 and chloroplastic CSD2) transcripts, which can detoxify Cu-induced oxidative stress. This also causes downregulation of transcription of miR398, which otherwise would have cleaved mRNA of CSD1 and CSD2. This results in posttranscriptional accumulation of mRNA of CSD1 and CSD2 (Sunkar et al. 2006). Expression of all the three miR398s ($miR398_a$, $miR398_b$, $miR398_c$) is downregulated in *Arabidopsis*, when exposed to excess of Cu. Expression of miR398s is induced due to Cu deficiency with concurrent downregulation of CSD1 and CSD2. Simultaneously Fe-SOD (FSD) is upregulated, which takes over dismutase function (Sunkar et al. 2006; Gielen et al. 2012). Such regulation is carried out by SPL7 (squamosa promoter-binding protein-like 7), which directly binds GTAC motifs of both FSD and miR398b/c promoters and upregulates their expression. This results in positive regulation of FSDs and negative regulation of CSDs (Abdel-Ghany and Pilon 2008, Yamasaki et al. 2009). A conserved KIN17, curved DNA-binding domain protein, assembles with SPL7 to adapt *Arabidopsis* growth and development to limiting copper availability (Garcia-Molina et al. 2014).

The *Arabidopsis* genome contains 17 members of laccase genes. A total of seven members of genes of laccase family are targeted by miRNAs, miRNA397, miR408, and miR857, due to Cu deficiency. Higher plants probably prioritize the delivery of copper to essential copper proteins by downregulation of nonessential or replaceable copper-containing proteins by miRNA. This could be an essential part of the copper homeostasis mechanism that allows plants to cope with variable copper supply and that, therefore, broadens the range in which plants can thrive (Abdel-Ghany and Pilon 2008).

22.4.8 *Manganese (Mn^{2+})*

Mn can exist in various oxidation states (0, II, III, IV, VI, and VII). In biological systems Mn occurs preferably in the oxidation states of II, III, and IV (Guest et al. 2002). Mn deficiency is rarely observed in plants, since its cellular requirement is low. Typical concentration of Mn in plants is in the range of 20–500 μg g^{-1}. In plants Mn toxicity causes chlorosis and brown speckles on mature leaves and necrosis, which results in reduced yield (Marschner 1995). All the symptoms of Mn toxicity are caused due to its effects on photosynthesis of plants (Millaleo et al. 2010).

Experiments with use of ^{54}Mn (Page and Feller 2005; Page et al. 2006) on wheat and white lupine plants (*Lupinus albus)* show that 7 days after labelling phase, almost all ^{54}Mn moves to the youngest fully expanded leaves and only a small fraction to the other leaves. Mn accumulation is found in the periphery of old leaves. Roots release Mn rapidly into the xylem to reach the photo synthetically active leaves through the transpiration stream. Mn tends to accumulate primarily in shoots rather than in roots of plants.

22.4.8.1 Cellular Mn^{2+} Uptake and Homeostasis

The gene families involved in Mn transport include (i) cation/H^+ antiporters, (ii) Nramps, (iii) the ZIP family, (iv) the CDF family, and (v) P-type ATPases.

Cation/H^+ Antiporters The *Arabidopsis* AtCAX1 is a vacuolar high-affinity Ca^{2+}/H^+ antiporter. AtCAX2 has low affinity for Ca^{2+} and possibly transports Mn^{2+} and Cd^{2+} across the tonoplast (Hirschi et al. 1996; Hirschi et al. 2000).

Nramps In *Arabidopsis* out of six Nramp genes, five (*AtNramp1-4 and AtNramp6*) have been characterized at the molecular level. The transporters AtNramp1, AtNramp3, and AtNramp4 can transport Fe, Mn, and Cd. AtNramp1 acts as a high-affinity Mn transporter for Mn uptake by the roots when soil Mn concentration is less than 1 μM. *AtNramp1* is expressed in root plasma membrane and upregulated by Mn deficiency. Overexpression of *Nramp1* in plants enhances growth and increases Mn content of the plants under Mn-deficient conditions (Cailliatte et al. 2010). *OsNramps5* is involved in transport and uptake of Mn, Fe, and Cd by rice (Ishimaru et al. 2012).

The ZIP Family Milner et al. (2013) studied 11 members of ZIP family of *Arabidopsis*. They report from yeast complementation studies that, possibly, ZIP7 can transport Zn, Mn, and Fe; ZIP1 and ZIP2 transport Zn and Mn; ZIP3, ZIP11, and ZIP12 transport Zn alone; ZIP5, ZIP6, and ZIP9 transport Mn alone; and none can transport Cu. IRT1, a member of ZIP family, is a high-affinity Fe^{2+} transporter under Fe-deficient conditions but also transports a number of other cations including Mn (Eide et al. 1996; Vert et al. 2002). In a Mn-efficient genotype of barley, expression of IRT1 is found to be about 40% greater suggesting existence of an efficient Mn uptake system (Pedas et al. 2008).

The CDF Family The proteins of this family are involved in efflux of transitional metal cations, Zn^{2+}, Cd^{2+}, Co^{2+}, Ni^{2+}, or Mn^{2+}, from cytoplasm to outside of the cell or into subcellular compartments to maintain metal homeostasis and tolerance to their toxic effects (Hall and Williams 2003; Hanikenne et al. 2005).

22.4.8.2 miRNA and Abiotic Stress due to Mn

In a study to identify Mn-responsive miRNAs in common bean (*Phaseolus vulgaris*), Valdes-Lopez et al. (2010) report that out of a total of 37 miRNAs with differential expression due to abiotic stress including Mn stress, 11 miRNAs are induced and another 11 miRNAs are inhibited under Mn stress. miR1508, miR1515, miR1510/miR2110, and miR1532 are characterized as Mn-responsive, and their targets are predicted as calcium-dependent protein kinase, heat-shock proteins, nucleoside-binding site leucine-rich repeat resistance-like proteins, and receptor kinase protein, respectively (Valdes-Lopez et al. 2010).

22.4.9 Boron (B)

Boron concentration in monocots varies between 6 and 18 μg g^{-1} and in dicots from 20 to 60 μg g^{-1}. Boron deficiency occurs at <20 μg g^{-1} B in mature leaf tissues. B is not readily translocated from older to younger leaves. The first visual symptom is cessation of terminal bud growth and death of young leaves. Young leaves become pale green in color and have twisted appearance. There is rotting of fruits, tubers, or roots leading to formation of darkened areas called black hearts. Plants are more sensitive to boron deficiency in the reproductive stage than in vegetative stage. Boron is essential for cell wall structure and functions. Primary cell wall of higher plants consists of cellulose, hemicelluloses (xyloglucan and arabinoxylan), and pectic polysaccharides, which consist of galacturonic acid-rich polysaccharides that form a hydrated matrix in which cellulose-hemicellulose network is embedded. The major components of pectic matrix are homogalacturonan (HG), rhamnogalacturonan-I (RG-I), and rhamnogalacturonan-II (RG-II). Boron forms cross links in pectic polysaccharides through borate-diol bonding of two rhamnogalacturonan-II (RG-II) molecules in the cell wall. RG-II is present in primary cell wall.

B toxicity causes chlorotic leaves with necrotic patches often in the margins and tips of older leaves. B toxicity in fruits manifests itself in the form of gummy nuts, internal necrosis and stem die back. Boron concentration in root tissues generally remains low and roots appear not to be affected by B toxicity.

22.4.9.1 Boron Stress and Cellular B Homeostasis

Boron exists primarily as boric acid, $B(OH)_3$, in soil solution. Boric acid is a weak Lewis acid with a pKa of 9.24. At a soil pH >9.0, boric acid forms $B(OH)_4^-$ ion (Woods 1996).

$$B(OH)_3 + H_2O = B(OH)_4^- + H^+$$

H_3BO_3 is the preferred form in which roots absorb B. Boric acid is permeable through lipid bilayer. It was thought prior to 1990 that B uptake by plants is through passive transport without any support of protein transporters. Casparian strips are not fully developed in root tips and solutes can get into the xylem by apoplastic flow, an important pathway for Ca^{2+} transport to shoots (White 2001). Casparian strips are hydrophobic lipid layers (suberin) present in the cell wall between the endodermal cells, which block apoplastic flow of solutes into the stele. Nutrient uptake by plants through most of its root length involves transport through plasma membrane and Casparian strips twice, once getting into the cell and then exporting out of the cell into the xylem. Two types of protein transporters are required for such symplastic flux, one for influx and another for efflux of solutes (Miwa and Fujiwara 2010).

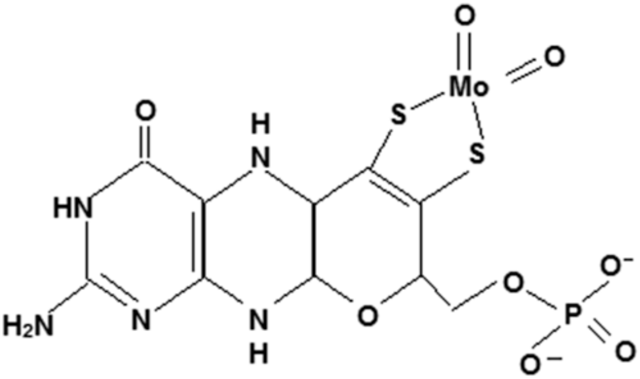
The transporters, involved in symplastic influx of B, are aquaporins such as NIP5;1 (nodulin-26-like intrinsic proteins), localized in the plasma membrane and upregulated under B-limiting conditions, which facilitates B influx into the root cells (Takano et al. 2006), and NIP6;1, involved in transfer of boric acid from xylem to phloem in the nodal regions (Tanaka et al. 2008). BOR1 and BOR4 are efflux transporters.

Boron transporters such as, HvBor2/Bot1 in barley, TaBOR2 in wheat, and AtBOR4 of *Arabidopsis* efflux excess B from plant cells and make them tolerant to B toxicity (Reid 2007). It has been reported that tolerant cultivars of barley and wheat show necrosis of leaves at higher leaf B concentrations. However, leaf protoplasts contain lower B concentration. Boron transporters probably efflux toxic boron out of the cell to the apoplast and protect the cytoplasm of the leaf cells from B toxicity (Reid and Fitxpstrick 2009).

22.4.10 Molybdenum (Mo)

Plants containing <0.2 μg g^{-1} are likely to show Mo deficiency. However, this concentration may vary in different plant species. Mo toxicity is rare under field conditions. Forage crops with high molybdenum may occur in wet, high pH, and high organic matter soils. Cattle consuming such forage may suffer from a disease called molybdenosis. This disease is caused by an imbalance in Mo and Cu in their diet if Mo content is more than 5 μg g^{-1}. Mo toxicity causes stunted growth and bone deformation in animals, which may be cured by oral feeding of Cu.

Mo is taken up by plants as MoO_4^{-2}, which is then used for synthesis of pterin-based Mo cofactor (Moco). Mo in Moco is covalently bound to two S atoms of a unique tricyclic pterin moiety known as molybdopterin. All forms of life contain Mo enzymes, which are involved in global cycling of C, S, and N. All of these enzymes are activated by Moco except nitrogenase. Moco becomes unstable when it is dissociated from the protein part of the enzymes (Basu and Burgmayer 2011). The Moco-containing enzymes found so far in plants consist of (1) nitrate reductase, NR; (2) sulfite oxidase, SO; (3) xanthine dehydrogenase, XDH; and (4) aldehyde oxidase, AO.



Structure of Moco. (Adapted from Mitra 2015)

22.4.10.1 Molybdenum Stress and Homeostasis

A member of group V sulfate transporter, Sultr 5;2, is probably an intracellular transporter involved in Mo (molybdenum) metabolism in *Arabidopsis* and is named as MOT1. MOT1 is a high-affinity molybdate transporter specific for Mo and allows plant to take up Mo from the scarce resource of Mo in soil. It is expressed in all tissues of wheat (Shinmachi et al. 2010). Mo deficiency affects N and S metabolism in a manner different from N and S deficiency. Studies with rice seedlings indicated that Mn^{2+}, Zn^{2+}, Cu^{2+}, Cl^-, or SO_4^{2-} reduced MoO_4^{2-} uptake, but Fe^{2+} had a positive effect (Kannan and Ramani 1978). There is a significant accumulation of phosphate in plants due to Mo deficiency. This is caused by induction of *PHO;H1* (a member of *PHO1* family) and its expression in roots of Mo-deficient plants. *PHO1;H1* is involved in phosphate acquisition and induced by phosphate deficiency (Stefanovic et al. 2007). Phosphate deficiency has been reported to enhance Mo uptake in tomato plants (Heuwinkel et al. 1992).

22.4.11 Nickel (Ni^{2+})

Nickel (Ni) becomes available to plants in the form of Ni^{2+} ions. Ni is readily oxidized in soil and becomes unavailable to plants above pH 6.7. Soils rich in Zn and Cu may also show Ni deficiency. Ni concentration of plant leaves is in the range of 0.05–5 mg kg^{-1}. Ni deficiency results in delayed nodulation and reduced efficiency in nitrogen fixation in leguminous plants (Brown 2006). Ni concentration >10 μg g^{-1} is generally considered toxic to sensitive plants.

22.4.11.1 Nickel Stress

Nickel is a constituent of enzyme urease (Dixon et al. 1975), which is present in a large number of plants. It has been observed in several plants that Ni deficiency results in accumulation of toxic concentration of urea in the leaves due to depression of urease activity. Nickel acts as a cofactor of enzyme urease and is essential for conversion of urea into NH_4^+ for use by plant tissues.

$$NH_2.CO.NH_2 + 3H_2O \underset{Urease}{\overset{Ni}{=}} 2NH_4^+ + CO_2 + 2OH^-$$

It has been suggested that AtIRT1, of ZIP family, which is a high-affinity Fe transporter by roots of *Arabidopsis*, also transports Ni (Nishida et al. 2011). There is a negative interaction between Ni and other nutrients such as Zn, Cu, Mn, Fe, Ca, or Mg, and higher concentration of any of these or along with others may cause Ni deficiency in soil (Liu et al. 2012).

22.4.12 Chloride (Cl^-)

Concentration of chloride in higher plants is usually 0.2–2.0% but may go up to 10% in saline soils (Fixen 1993). Chloride-deficient leaves show wilting, chlorosis, necrosis, and an unusual bronze discoloration. Cl^- can be toxic to plants if its concentration exceeds 4–7 mg g^{-1} of dry weight for chloride-sensitive species and 15–50 mg g^{-1} for chloride-tolerant plants (Xu et al. 2000).

22.4.12.1 Chloride Stress

While both Na^+ and Cl^- are toxic at higher concentration, some plants can regulate Na^+ uptake better than Cl^- (Munns and Tester 2008). High Cl^- concentration causes chlorophyll degradation and reduces actual quantum yield of PSII electron transport (Pokhrel et al. 2011). Capacity to control Cl^- exclusion from shoots has been correlated with salt tolerance in many species of plants (Teakle et al. 2007; Teakle and Tyerman 2009).

Minimum concentration of chloride in plant tissue essential for biochemical reactions is about 100 mg kg^{-1} of dry wt. Chloride is a major osmotically active ion in the vacuole and is involved in turgor and osmoregulation.

22.4.12.2 Chloride Uptake and Homeostasis

Influx of Cl^- into the symplasm appears to be active, whereas efflux is passive since there is a gradient for passive efflux of anions from cytoplasm to the external medium (Teakle and Tyerman 2009). Both active and passive Cl^- transport occurs through tonoplast. Electrophysiological studies indicate the presence of $Cl^-/2H^+$ symporter in the plasma membrane of root hair cells and Cl^-/nH^+ antiporter mediates chloride influx across tonoplast. Genes of chloride channels (CLCs) from plants have been cloned from tobacco, *Arabidopsis*, rice, and soybean. All of them belong to the family of voltage-gated chloride channel and are generally expressed in endomembranes of all tissues. There are seven members of this family in *Arabidopsis* (*AtCLC(a), (b), (c), (d), (e), (f), and (g)*) and rice (*OsCLC 1–7*). In *Arabidopsis* AtCLC(a), protein is expressed in the tonoplast; AtCLC(d), trans-Golgi; AtCLC(f), cis-Golgi; and AtCLC(e), thylakoid of chloroplast.

22.5 Beneficial Plant Nutrients and Abiotic Stress

These include Na, Co, Si, Se, and V. Some of them are essential for some of the plants, but others are beneficial to a few plants and animals who consume these plants.

22.5.1 Sodium (Na^+)

Na^+ is not an essential nutrient for all plants. It is essential for halophytes, which accumulate salt in vacuoles to maintain turgor and growth. A few of the C4 plants (except corn and sorghum) need Na^+ essentially for specific functions, such as in the concentration of $CO_{2.}$ Na^+ can be beneficial to plants under conditions of K^+ deficiency. Na^+ can undertake osmotic functions, reduce the total K^+ requirements and improve growth when the lack of K^+ is a limiting factor. A near complete replacement of K^+ by Na^+ in its osmotic function is possible. Improvements of some of the quality parameters due to addition of Na^+ have been reported, such as greener leaves, glossy leaves caused by increase in cuticular wax formation (Brownell and Crossland 1972), and improvement of taste and texture of crops (Zhang and Blumwald 2001).

In sugar beet Na^+ concentration in leaf tip may increase up to 10%. Na^+ has effect on water relations and increases drought resistance of sugar beet. In Na^+-deficient soils, beet leaves are dark green, thin, and dull in hue.

22.5.1.1 Sodium and Drought Stress

High Na^+ concentration is toxic to plants especially under drought and causes dehydration of roots. Na^+ can replace Ca^{2+} in the plasma membrane under sodic conditions resulting in increase of membrane permeability and transport of ions (Bresler et al. 1982). Na^+ toxicity is primarily exhibited in the shoots, where Na^+ accumulation disrupts metabolic processes and increases osmotic stress on cells (Munns 2002). Sudden increase in Na^+ concentration has osmotic consequences disrupting membrane integrity of roots in crops (Britto et al. 2010) and of shoots in rice (Flowers et al. 1991). Na^+ disrupts K^+ influx and homeostasis both at high- and low-affinity ranges especially at mM concentrations (Kronzucker et al. 2006). Vacuole tolerates replacement of K^+ by Na^+ due to sequestration of Na^+ by transporters such as NHX, which does not harm cytosolic functions (Munns and Tester 2008).

22.5.1.2 Cellular Na^+ and K^+ Homeostasis

High-affinity Na^+ uptake is mediated by HKT transporters in rice, species of Triticeae and Aveneae tribes of Poaceae family (Haro et al. 2010). *OsHKT2;1* is involved in high-affinity Na^+ transport under K^+-starved conditions and can partially replace K^+. *OsHKT2;2* catalyzes Na^+-dependent K^+ uptake. In rice, barley, and wheat, expressions of transcripts that encode HKT transporters significantly increase under K^+-starved conditions, and Na^+ uptake is inhibited by addition of K^+. In sunflower plants Na^+ uptake is not K^+-sensitive. No other transporter has been conclusively proved to be involved in high-affinity Na^+ uptake by plants.

22.5.2 Silicon (Si)

Silicon occurs in soil solution primarily as H_4SiO_4 (orthosilicic acid) at a concentration of 0.1–0.6 mM and is taken up by plants in this form (Epstein 1994). Silicon (Si) is a constituent of all plants and its concentration in shoot may vary from 0.1% to 10% of dry weight. Si is the only element, which does not have any adverse effect when it accumulates in excess (Epstein 1999).

Si deficiency symptom in rice includes soft droopy leaves, reduced photosynthetic efficiency due to mutual shading of leaves, and reduced starch formation leading to incomplete grain filling.

Beneficial effects of Si application include increasing canopy photosynthetic efficiency by keeping leaves erect and compact; increasing resistance to fungi, bacteria, and insects; reducing toxicity to heavy metals; improving water use efficiency by reducing cuticular transpiration; and increasing resistance to lodging.

22.5.2.1 Si and Abiotic Stress

Mn Toxicity High concentrations of Mn in plants increase superoxide dismutase, catalase, and ascorbate peroxidase activities but decrease concentrations of nonprotein thiols and glutathione, which results in accumulation of $OH^{\cdot}$ and malondialdehyde. Addition of Si has been observed to significantly neutralize Mn-induced increase in $OH^{\cdot}$ and malondialdehyde and enhance plant growth in rice (Li et al. 2012).

Al Toxicity Silicon has been reported to alleviate Al toxicity in conifers, barley, soybean, maize, and sorghum. Formation of non-phytotoxic hydroxyl aluminum silicates (HAS) in the apoplast of root apex detoxifies Al (Wang et al. 2004).

Silicon and Water Stress Under drought conditions there is closure of stomata and decrease in rate of photosynthesis. Si is deposited under the cuticle forming a Si-cuticle double layer. This reduces transpiration from cuticle of rice leaves. Si can reduce transpiration rate by 30% in rice, which has a thin cuticle (Ma et al. 2001, 2004). Treatment with Si increases percentage of ripened grains in rice (7% Si) and barley (1.5% Si) under water-stressed conditions (Ma 2004).

22.5.2.2 Si Uptake and Homeostasis

The Si uptake process involves two different types of transport, Si-permeable channel and efflux transporter (Yamaji et al. 2012). LSi1 (low silicon 1) is a member of NIP2 (nod 26-like major intrinsic protein2) subgroup of NIP subfamily of aquaporin-like proteins and functions as a Si-permeable channel (Yamaji et al. 2012). LSi2 functions as an efflux Si transporter and belongs to the anion transporter family without any similarity with LSi1. LSi6 is a homolog of LSi1 and is involved in xylem unloading of Si in rice (Yamaji et al. 2008).

22.6 Nonessential Ions and Abiotic Stress

Ions of elements such as Cr, W, As, Ag, Hg, Sb, Cd, Pb, and U with no known function in plant metabolism have been found to be taken up by plants. If the soil or growth medium is rich in one or more of the nonessential elements, these elements are likely to be taken up by plants to tolerable or sometimes toxic concentrations. These elements may be of geological origin or accumulated in the soil due to anthropogenic causes. Soils around mining sites or nearer to solid waste dumps from mineral-based industries may contain elements toxic to plants. Use of untreated effluents from industries and use of sewage and sludge from urban centers in agriculture as sources of irrigation and atmospheric deposits of radioactive isotopes from any overground nuclear activities on soils and plants are other sources of nonessential elements. When food crops are grown on these soils, the nonessential elements are likely to be taken up by the plants and may enter into the food chain of man and animals.

22.6.1 Heavy Metal Transporters

Some of the ion transporters, which are involved in uptake of essential nutrients, can transport ions of heavy metals with identical ionic geometry (Mitra 2015).

Heavy Metals ATPases (HMAs) HMAs belong to the P_{1B} subgroup of P-type ATPase superfamily, where ATP hydrolysis supports transport of ions across plasma membrane. HMAs are divided into two clusters, Cu cluster and Zn cluster. The transporters of Cu cluster transport Ag^+ ions along with Cu^+. The transporter of Zn cluster transports Co^{2+}, Cd^{2+}, and Pb^{2+} along with Zn^{2+}, when these ions are available in the growth medium (Axelsen and Palmgren 2001).

ABC Transporters (ATP-Binding Cassette) The ABC transporters consist of a large family found in all the three kingdoms. Some of them are involved in heavy metal detoxification. The ABC transporter YCF1 (yeast cadmium factor1) in *Saccharomyces cerevisiae* transports bis(glutathione), cadmium, and arsenic complexes GS_2Cd and GS_2As from cytoplasm to vacuole (Ghosh et al. 1999; Gueldry et al. 2003). In *Arabidopsis* AtABCC1 and AtABCC2 contribute to Cd^{2+} and Hg^{2+} tolerance (Park et al. 2012).

The Nramps (Natural Resistance-Associated Macrophage Proteins) These transporters are proton/metal symporters and have broad divalent metal substrate such as Fe^{2+}, Mn^{2+}, Cd^{2+}, Co^{2+}, Ni^{2+}, and Pb^{2+}(Gunshin et al. 1997; Nevo and Nelson 2006).

The Cation Diffusion Facilitator (CDF) Family These transporter proteins are involved in transport of transitional metals cations such as Zn^{2+}, Cd^{2+}, Co^{2+}, Ni^{2+}, or Mn^{2+}, from cytoplasm to outside of the cell or into subcellular compartments to maintain metal homeostasis and tolerance to their toxic effects (van Der Zaal et al. 1999; Hall and Williams 2003; Hanikenne et al. 2005).

The ZIP (ZRT IRT-Like Proteins) Family The ZIP transporters have been identified from a number of plants mainly dicots (Grotz and Guerinot 2006) and are involved in transport of metal ions such as Mn^{2+}, Fe^{2+}/Fe^{3+}, Cd^{2+}, Co^{2+}, Cu^{2+}, Ni^{2+}, and specifically Zn^{2+}.

The CAX Family (Cation/H^+ Antiporters) These are cation/H^+ antiporters involved in cation influx into the vacuole. They transport heavy metals such as Cd, Ni, and Mn into the vacuole and facilitate root growth under heavy metal stress conditions (Mei et al. 2009).

Higher plants have also built-in cellular mechanisms for metal detoxification and tolerance to protect them from uptake of toxic ions, such as (i) restriction of metal movement to roots by mycorrhizal association, (ii) binding the metals to cell wall and to root exudates, (iii) reduce influx across plasma membrane, (iv) active efflux into apoplast, (v) scavenging by root border cells, (vi) chelation in cytosols by various ligands, and (vii) transport of accumulated metals to the vacuole (Mitra 2015). Further there are interactions among nonessential and essential nutrients, which sometimes may be beneficial or harmful to the plants as discussed in earlier chapters.

22.6.2 Radioactive Isotopes and Abiotic Stress

Radioactive nuclides are a part of the terrestrial environment emanating from radioactive substances present in the earth's crust and from cosmic rays. Recently there has been enrichment of specific nuclides in the environment due to manufacture and testing of nuclear weapons, extensive construction of nuclear power plants, commercial fuel reprocessing, nuclear waste disposal, uranium mining and enrichment, and nuclear accidents. The radioactive nuclides released by nuclear weapon tests include the following:

$$^{140}\mathrm{Ba},\ ^{14}\mathrm{C},\ ^{141}\mathrm{Ce},\ ^{144}\mathrm{Ce},\ ^{137}\mathrm{Cs},\ ^{55}\mathrm{Fe},\ ^{3}\mathrm{H},\ ^{131}\mathrm{I},\ ^{54}\mathrm{Mn},\ ^{239}\mathrm{Pu},\ ^{241}\mathrm{Pu},\ ^{103}\mathrm{Ru},\ ^{106}\mathrm{Ru},\ ^{125}\mathrm{Sb},\ ^{89}\mathrm{Sr},\ ^{96}\mathrm{Zr}$$

Some of these and/or their daughter nuclides are released.

22.6.2.1 Major Accidents in Nuclear Power Plants

(a) Chernobyl in USSR, April 26, 1986, caused by explosion in nuclear power plant due to operational error

(b) Daiichi Fukushima, Japan, on March 11, 2011, due to meltdown of nuclear power plant damaged by tsunami

The four most harmful radionuclides released due to Chernobyl disaster were ^{131}I, ($t_{1/2}$ = 8.02 days, may cause thyroid cancer), ^{137}Cs ($t_{1/2}$ = 2.07 years, may accumulate in heart and cause circulatory disease), ^{134}Cs ($t_{1/2}$ = 30.2 years), and ^{90}Sr ($t_{1/2}$ = 28.8 years, may accumulate in bones). The radioactive nuclides monitored from Fukushima Daiichi explosions were ^{131}I and ^{137}Cs. The regulatory levels fixed by Japan were 2 Bq/g for ^{131}I and 0.5 Bq/g for ^{137}Cs. There were soil contaminations with these two nuclides. Soils of a large area of eastern and northeastern Japan were contaminated with ^{137}Cs. About 18 months after the Fukushima explosion, Health

Ministry data showed that radiation from Cs was not detectible in most of the vegetables. The trend was the same for beef. Rice harvested from Fukushima Prefecture was found to be safe (Aoki 2012). The distribution of absorbed radioactive ^{137}Cs in rice plants is 65% in straw, 10% in polished rice, 10% in bran, and 10% in husk (Tsukada et al. 2002). Studies on Cs uptake by plants indicate that the inwardly rectifying KIR and outwardly rectifying KOR and voltage-sensitive VIC channels are all permeable to Cs, also the high-affinity K^+/H^+, KUP/HAK/KT, symporters. VIC channels mediate most (30–90%) of Cs influx under physiological conditions, and the KUP/HAK/KT transporters mediate the bulk of the remainder, when the external concentration of Cs is below 200 μM (White and Broadly 2000).

Chernobyl accident data have shown that ^{137}Cs ($t_{1/2} = 30.2$ years) adsorbed on the top soil layer can remain there for long years making the soil unfit for crop production (Yasunari et al. 2011). High exposure to radiation from ^{137}Cs at Chernobyl caused radiation-induced thyroid cancer.

Soon after the Chernobyl disaster, four square Km of pine forest directly downwind of the reactor turned red and died. However subsequent to atom bomb blast in Nagasaki and Hiroshima, many trees such as gingko, black locust, and camphor survived and were still growing (Eckholm 1985). The radiation level caused by Chernobyl disaster is still very high, and 30 Km around the factory has been declared as “zone of alienation.” It may take 20,000 years to become fit for human habitation. The plants growing in the zone of alienation contain higher levels of ^{137}Cs.

The area however has reverted to become a natural forest and overrun by wildlife due to the lack of competition from humans for space and resources. This indicates that plants and animals can survive in a relatively high-radiation zone.

A study was conducted on progeny of *Arabidopsis* plant collected from zone of alienation with different levels of contamination. The study indicated a significantly higher resistance of progeny *Arabidopsis* plants to mutagens. There was increased expression of radical scavenging genes *CAT1* and *FSD3* and DNA repair genes *RAD1 and RAD51-like* in these plants (Kavalchuk et al. 2004).

According to World Nuclear Association (2015), the human environment has always been radioactive and accounts for 85% of annual radiation dose, 2.4 mSv/year. The radiation dose received from all nuclear activities accounts for less than 1%.

22.7 Climate Change and Nutrient Uptake

Plants regulate expression levels of different sets of genes to coordinate physiological and developmental responses to environmental changes (Nagano et al. 2012; Plessis et al. 2015). Plants rely on gene regulatory network to survive on growth-limiting conditions. Plant genomes encode a large number of TFs to survive abiotic stress since they are sessile. Many TF proteins exist in an inactive form in the cytosol or nucleus until they are activated by developmental or environmental signals (Fu et al. 2011; Ohama et al. 2016). Wilkins et al. (2016) used environmental gene regulatory influence networks (EGRINs), which included regulatory interactions between 4052 target genes regulated by 113 TFs. They observed distinct regulatory role for members of the heat-shock factor family and regulatory connection between abiotic stress and circadian clock. For domesticated crops like Asian rice (*Oryza sativa*), understanding EGRINs can ensure high yields under a range of climatic conditions (Mickelbart et al. 2015; Olsen and Wendel 2013).

A study on effects of elevated CO_2 on plant carbon, nitrogen, and water relations showed that:

(i) Carbon uptake is enhanced by elevated [CO_2] despite acclimation of photosynthetic capacity.
(ii) Photosynthetic nitrogen use efficiency increases at elevated [CO_2].
(iii) Water use at both leaf and canopy scales declines at elevated [CO_2].
(iv) Dark respiration is significantly stimulated in soybean leaves grown under elevated [CO_2].
(v) Stimulation of carbon uptake by elevated [CO_2] in C4 plants is indirect and occurs only in situations of drought.
(vi) The [CO_2] "fertilization" effect in FACE studies on crop plants is less than expected (Leaky et al. 2009).

At an elevated CO_2 concentration (550 μM/M), protein content of wheat decreased by 12.7%, and there were decreases in S, Ca, Fe, and Zn content as well (Fernando et al. 2012). A 2-year study using the FACE (free-air CO_2 enrichment) and warming facility showed that total crop N content increased with increase in temperature, but N allocation to the leaves and to Rubisco was reduced by elevated temperature and higher CO_2 concentration at mid-grain filling stage. This resulted in a strong downregulation of leaf photosynthetic rate. The changes in N allocation resulted from changes in phenology and/or senescence accelerated by warmer soil and water. There is a need for integrated and quantitative understanding of the ecosystem-based response to elevated CO_2 concentration and increase in temperature (Adachi et al. 2014).

There are very limited studies on effect of global warming on nutrient transporters. Giri et al. (2017) studied effect of moderate and severe short-term heat stress on nutrient uptake by roots of tomato (*Solanum lycopersicum* L, Cv: Big boy). They examined effects on high- and low-affinity nitrate transporters NRT2 and NRT1, the primary ammonium transporter AMT1, primary root phosphate transporter PHT1, potassium transporter KT1, iron uptake protein in dicots, iron reductase FRO1, and two boron transporters, BOR1 and NIP5;1. Further they also studied the effects of heat on N assimilation enzymes, nitrate reductase (NR), glutamate dehydrogenase (GDH), glutamine synthetase (GS), and glutamine oxoglutarate aminotransferase (GOGAT). As compared to control plants, heat stress (35°C and 42°C) initially decreased concentration (per gram of dry root) of all the nutrient uptake proteins (NRT1, NRT2, PHT1, KT1, FRO1, BOR1, NiP5;1). After 6 days of heat stress, the moderately stressed plants had similar level of nutrient uptake proteins as untreated control. In severely heat-stressed plants, these proteins were at a lower level than control except NIP5;1 and AMT1. After 7 days of post heat recovery, all the plants had similar levels of transporter proteins as control except FRO1. Similarly, all the nutrient assimilation proteins decreased due to initial heat stress but recovered gradually as the heat stress was withdrawn. These results indicate that nutrient uptake by plants can withstand temporary heat stress and nutrient assimilation recovers once weather becomes normal.

Climate change variables primarily include (i) increase in atmospheric CO_2 concentration, (ii) increase in global temperature, and (iii) uncertain precipitation. While increase in CO_2 concentration has positive effect on crop yield and hence uptake of plant nutrients, temperature increase has a negative effect on crop yield and nutrient uptake. Thermotolerant varieties of crop plants could be evolved, which can take up nutrients at a moderately higher temperature. However, the third variable, precipitation, will have the controlling effect on nutrient uptake. Plant nutrients are taken up in an aqueous medium. The AQP genes are involved in water uptake. High N application to rice has been reported to result in increased transcription level of aquaporins, increased rate of water uptake and the root hydraulic conductance and decreased aerenchyma formation (Ren et al. 2015). A study on rice (Liu et al. 2006) indicates that water channels and K^+ channels/transporters have potential functional correlations. The mRNA expression levels of plasma membrane intrinsic proteins (PIPs) and K^+ channel/transporters responded similarly to K^+ starvation or water deprivation. Such inbuilt interactions in plants are valid for moderate drought conditions but cannot sustain nutrient uptake under localized climate change extremes.

Adaptation to moderate changes in climate that influence temperature, season length, and planting dates, as well as the occurrence of abiotic stress, can be achieved by selecting varieties with appropriate flowering times and crop durations. Plants rely on gene regulatory network to survive on growth-limiting conditions. As discussed earlier understanding EGRINs can ensure high yields under a range of climatic conditions (Mickelbart et al. 2015; Olsen and Wendel 2013).

22.8 Conclusion

An elaborate gene regulatory mechanism exists in plants to ensure uptake of water and essential plant nutrients and maintain cellular homeostasis under conditions of abiotic stress. There are groups of genes for every nutrient, which encode transporter proteins whose functions are to acquire specific nutrient from the soil and transport them across the plasma membrane of the root hair cells for use in plant metabolism. Deficiency or sufficiency of a plant nutrient induces different sets of genes to produce mRNA transcripts for translation of transporter proteins. There are early and late genes, which are expressed, when nutrient deficiency is for a short or for a prolonged period. Several genes, which encode transporter proteins for each of the essential plant nutrients, have been identified and their transporter proteins characterized. There are groups of transporters, which transport more than one nutrient. Some of them also transport nonessential heavy metals. Under nutrient-deficient conditions, plants reprioritize their internal use and recycle them from older to new tissues. Cellular homeostasis of the micronutrients, which become toxic beyond a threshold concentration, is achieved by regulatory mechanisms, such as intracellular binding by metal chelators (mugineic acid, phytochelatins, metallothioneins), efflux from the cell, and sequestration into vacuoles. There are also protective mechanisms for highly active nutrients (Cu chaperons) from improper interaction with other cellular constituents.

Globally the soils are deficient in one or more of the primary nutrients, N, P, and K, which are required in larger quantities for crop production. Their nutrient use efficiency by crops for these nutrients is low, which results wastage of a larger portion of applied nutrients. The unutilized nutrients also cause environmental pollution. Efforts to develop transgenic crops with improved nutrient use efficiency have so far been partially successful but far from their use under field conditions. There have been attempts to enrich food crops with some of the micronutrients. Iron deficiency is a major health problem for humans around the world. About 25% of world population suffer iron deficiency. About one third of world's population suffer from zinc deficiency, which causes impaired brain development, dysfunction of reproductive system, immune disorders, hair loss, skin lesions, and loss of taste and smell. Genetic information available on mechanism of nutrient uptake can be fruitfully utilized to develop food crops with superior nutritive values.

The climate change scenario will have its effect on nutrient uptake by plants. New crop varieties, which can take up nutrients under altered climate change conditions and produce enough to meet the requirements of human and animal, have to be developed.

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